Museum KOENIG

LIB Leibniz-Institut zur Analyse des Biodiversitätswandels

Bonn zoological Bulletin

Volume 72
Issue 2
2023

formerly: Bonner zoologische Beiträge

An open access journal of organismal zoology, published by
the Leibniz Institute for the Analysis of Biodiversity Change (LIB) – Museum Koenig, Bonn

BHL

Blank Page Digitally Inserted

LIB Leibniz Institute for the Analysis of Biodiversity Change
Museum KOENIG
Bonn zoological Bulletin 72 (2): 163–184
2023 · Bates M.F.
https://doi.org/10.20363/BZB-2023.72.2.163

ISSN 2190–7307
https://www.zoologicalbulletin.de

Research article

urn:lsid:zoobank.org:pub:9530135C-50BE-4F8C-8219-AB26D8CFF31F

The enigmatic Namibian egg-eating snake *Dasypeltis loveridgei* Mertens, 1954 (Squamata: Colubridae): A valid species recovered from synonymy

Michael F. Bates

Division of Herpetology, Department of Animal and Plant Systematics, National Museum, P.O. Box 266, Bloemfontein 9300, South Africa
Department of Zoology & Entomology, University of the Free State, P.O. Box 339, Bloemfontein 9300, South Africa
Corresponding author: Email: herp@nasmus.co.za
urn:lsid:zoobank.org:author:91DE76EE-29CD-4CFB-AB14-DE91DC2135F2

Abstract. A subspecies of egg-eating snake, *Dasypeltis scabra loveridgei* Mertens, 1954, from Namibia, has been considered a junior synonym of *Dasypeltis scabra* (Linnaeus, 1758) by most authors since 1983. A detailed morphological analysis of 153 preserved museum specimens from Namibia was conducted in order to re-evaluate the taxonomic status of egg-eaters in the country. Two distinct morphotypes, 'scabra' and 'loveridgei', were identified. In Namibia, *Dasypeltis loveridgei* is typically distinguished from *D. scabra* as follows: mid-dorsal saddles in the form of dark brown hourglass-shaped markings (versus quadrants, ovals or irregular shapes); belly with a single row of dark markings at the edges (versus 2–3 rows or heavily marked); six supralabials on either side of head, 2nd and 3rd in contact with the orbital (versus 7 [3,4]); internasals longer (versus shorter) than the prefrontals; top of rostral barely visible when head is viewed from above (versus clearly visible); frontal often smooth to moderately pitted (versus usually largely to extensively pitted); inter-prefrontal sulcus weakly marked or moderate (versus often deep and distinct). *Dasypeltis scabra* occurs in central and north-eastern Namibia, with a single record in the south-west which may be associated with populations in the Northern Cape Province of South Africa; *D. loveridgei*, which is here shown to be a valid species, is widespread in the country, excluding the north-east, but largely restricted to areas above 1000 m a.s.l. The two species are sympatric at a few localities in central Namibia, and parapatric in several areas throughout the country.

Key words. Serpentes, Colubrinae, *Dasypeltis*, egg-eating snake, taxonomy, Namibia.

INTRODUCTION

The 17 recognised species of egg-eating snakes, *Dasypeltis* Wagler, 1830, are widely distributed in Africa (excluding most of the Sahara) – including isolated populations at Fayum in Egypt, in Morocco and Western Sahara, and in Sudan – and in the western parts of the Arabian Peninsula (Bates & Broadley 2018; Escoriza 2012; Gans 1959, 1964; Saleh & Sarhan 2016; Trape & Mané 2006; Trape et al. 2012, 2021; Uetz et al. 2022). Currently, most authors recognise only three species in southern Africa, namely *Dasypeltis scabra* (Linnaeus, 1758), *Dasypeltis inornata* A. Smith, 1849, and *Dasypeltis medici* (Bianconi, 1859) (Bates et al. 2014; Branch 1998; Broadley 1990; Marais 2004, 2022), with only *D. scabra* recorded from Namibia.

Werner (1902) examined material from Windhoek and was the first author to note that in Namibia, *Dasypeltis* may have a similar dorsal pattern to that of the dwarf adder *Bitis caudalis* (A. Smith, 1839). Sternfeld (1908, 1910a–c) discussed the colour pattern of such Namibian egg-eaters in more detail and considered them to be mimics of *B. caudalis*. More than forty years later, Mertens (1954) described *Dasypeltis scabra loveridgei* based on a series of 10 specimens from central Namibia. He differentiated it from typical *D. scabra* by the hourglass-shaped dorsal markings along the middle of the back (similar to *B. caudalis*), and also suggested that it had greater numbers of ventral scales (212–218 in males, 225–230 in females).

In his revision of the genus *Dasypeltis*, Gans (1959) examined the paratypes of *D. s. loveridgei* and acknowledged their distinctive dorsal markings, referring to this pattern as '6N'. He added that high frequencies of the supralabial formula 6 [2,3] (i.e., six supralabials on either side of head, with 2nd and 3rd in contact with the orbital) occurred in southern Namibia, but that this became less common progressively northwards in the country. Gans (1959) also noted that ventral counts for 'loveridgei' were included within the range of variation of *D. scabra*, and he therefore referred *D. s. loveridgei* to its synonymy.

FitzSimons (1962) subsequently recognised *D. s. loveridgei* from the central highlands of Namibia (his record for Tsumkwe in the north-east is referable to *D. scabra*, see below) and noted that although it was indistinguishable from *D. s. scabra* in southern Africa with regards

Received: 12.09.2022
Accepted: 15.06.2023

Corresponding editor: W. Böhme
Published: 08.08.2023

to scalation, it differed markedly in terms of its colour pattern, most especially its possession of 42–54 hourglass-shaped markings on the back from nape to vent (usually squarish to rhomboical markings in *D. s. scabra*), with rectangular markings on the flanks (usually irregular vertical bars or stripes in *D. s. scabra*), and uniformly white underparts (often with dark spots in *D. s. scabra*). He also noted that *D. s. loveridgei* was apparently a smaller form, the longest known specimen measuring 663 mm in total length (585 mm snout-to-vent + 78 mm tail length); and that it had been suggested that (p. 180) "…tail length [of *loveridgei*] is on average shorter than in typical *scabra*, but this is open to some doubt and remains to be proved by measurements of a long series of correctly sexed specimens." FitzSimons (1962, 1966, 1970, 1974) did in fact, apart from colour pattern, use relative tail length to separate the two subspecies, i.e., total length/tail length: 5.3–6.8 in *D. s. scabra* and >7 in *D. s. loveridgei*.

For his revision of *FitzSimons' Snakes of Southern Africa*, Broadley (1983) examined 56 specimens of *Dasypeltis* from Namibia. He noted that specimens with the 'loveridgei' pattern and those with a pattern intermediate between this and the typical *D. scabra* pattern varied considerably with regards to colour pattern, ground colour (between the dark markings), ventral counts, subcaudal counts, and upper labial formula (see below), but "there was no correlation between these characters" (p. 265). He added that: "Recognition of *D. scabra loveridgei* as a formal subspecies is not justified, it is better treated as a colour phase, apparently developed in mimicry of *Bitis caudalis*."

As part of a revision of the genus *Dasypeltis* in the southern half of Africa, data from a sample of 153 Namibian specimens was analysed. Most specimens with mainly 'hourglass' markings on the back also had the supralabial formula 6 [2,3] (usually 7 [3,4] in *D. scabra*), which led me to question Broadley's (1983, 1990) decision to relegate *D. s. loveridgei* to the synonomy of *D. scabra*. Apart from dorsal colour pattern and the supralabial formula, several additional characters were also examined, some of which also proved useful in distinguishing between the two morphotypes.

Bates & Broadley (2018) proposed elevating *D. s. loveridgei* to full species status based on a combination of the unique dorsal colour pattern and usual supralabial formula of 6 [2,3] of several Namibian specimens as determined by Mertens (1954, 1955) and Gans (1959); and they also included Namibia in the distribution range of *D. scabra*. *Dasypeltis loveridgei* was until recently listed as a subspecies of *D. scabra* by The Reptile Database (Uetz et al. 2022). The present study provides data supporting the proposal that *D. loveridgei* is a valid species, and shows that this species and *D. scabra* are both fairly widespread in Namibia.

MATERIALS AND METHODS

Study area

Namibia is a largely arid country in south-western Africa situated between latitudes 16° 45' and 29° S, and lying mostly to the west of longitude 21° E, although it also includes the relatively narrow north-eastwardly extension known as the Zambezi Region (formerly Caprivi Strip). Although much of the country is arid, including the Namib Desert in the west and the western edge of the Kalahari Desert in the east, the north-easterly parts (especially the Kavango-Caprivi region) are subtropical, receive much more rainfall, and comprise forested savannah and woodland (Anon 2022). Much of the rest of the country consists of some form of savannah or shrubland. The Great Escarpment, including the Khomas Highland in the Windhoek region, runs north to south in the country and separates the western coastal areas (Namib) from the central plateau.

Material examined

Data on size, colour pattern and scalation for a total of 153 specimens of Namibian *Dasypeltis* and for comparison, eight *Dasypeltis confusa* Trape & Mané, 2006 (identification based on data in Trape & Mané 2006, Bates & Broadley 2018 and Trape et al. 2021) from Angola and south-western Democratic Republic of the Congo, from museums in southern Africa, Europe and the United States are presented in Appendix I. This includes data from material examined by the author (values in bold in Appendix I); as well as data from Mertens (1954, holotype: museum number marked by superscripted '1' in Appendix I), Gans (1959, appendix 1: superscripted '2' in Appendix I) and spreadsheets sent by the late Donald G. Broadley (some of this data, recorded using the same methods as in the present study, was probably used for the conclusions reached by Broadley 1983: superscripted '3' in Appendix I). Several of the above-mentioned specimens were examined by the author for at least some characters, and such data is also denoted in bold in the appendix. In some cases the author's data differs from that presented by Mertens (1954) and Gans (1959). For the holotype and most of the paratypes of *D. s. loveridgei*, as well as six *Dasypeltis* specimens in the Field Museum of Natural History (excluding FMNH 77610), photographic images were examined and data obtained in this way is also indicated in bold in Appendix I. Unless otherwise indicated, when museum specimen numbers are separated by an en dash, this implies a series (e.g., TMP 48337–9 refers to specimens 48337, 48338 and 48339).

Specimens were examined under a binocular dissecting microscope, or with the aid of magnifying lenses for some large specimens (D.G. Broadley, pers. comm.). One decapitated specimen (NMWN 3189b: Ja Dennoch, Kehoro Suid) could not be identified to species level because too few diagnostic characters were available. In the species accounts, localities (with museum specimen numbers) are listed alphabetically, and the mapping notation (e.g., 2616CB) refers to quarter-degree units (see usage in Bates et al. 2014: 8). Specimens listed as '*Dasypeltis* cf. *loveridgei*', although similar to *D. loveridgei*, were not included in the analysis as their taxonomic status is uncertain and currently under investigation (Bates et al. in prep.), but their localities were mapped.

Because of known differences in numbers of ventral and subcaudal scales between males and females of *Dasypeltis* (e.g., Bates & Broadley 2018; Broadley 1983, 1990; Gans 1959), an attempt was made to determine the sex of all specimens. Sex was determined by presence/absence of (one or both) inverted hemipenes (slit open to reveal spines if not obvious) in the tail base, presence of everted hemipenes, and/or presence of internal reproductive structures (males: testes, sperm ducts; females: eggs, ovaries, oviducts). Only sexed specimens were used for the analyses of relative tail length, and numbers of ventrals, subcaudals and midbody scales.

Characters used

Characters mentioned by previous workers (Broadley 1983; FitzSimons 1962; Gans 1959; Mertens 1954), including all those regarding differences or similarities between *D. scabra* and *D. loveridgei*, were examined and evaluated, together with a few additional characters (see Appendix I). Firstly, the dorsal, lateral and ventral colour patterns were determined. Dorsal pattern was usually identified as '5N' (*scabra*-like) or '6N' (*loveridgei*-like) with reference to Gans (1959), but variation in this regard is discussed. Lateral markings were generally categorised as elongate (typical for *D. scabra*), or squarish or irregular (not distinctly elongate; typical of *D. loveridgei*). Colour pattern on the belly (white to cream) was recorded as immaculate; with one, two or three rows of dark markings at the sides of the belly (not all ventral plates were necessarily marked, and if a single row was present then the markings were at the extreme edges of the plates adjacent to the lateral scales); or extensively marked. The rows of dark markings sometimes extended onto the tail.

Ventrals were counted from the first plate following the posterior (usually second) pair of chin shields, up to but excluding the anal plate (first ventral is always wider than long and usually similar to the next ventral; small extranumerary scales sandwiched between posterior chin shields were not included). Subcaudals were counted from the first adjoining pair behind the vent up to the pair in contact with the terminal spine (spine excluded). Longitudinal dorsal scale rows ('midbody scale rows') were counted at or near midbody (halfway between tip of snout and vent), usually by starting the count caudad and reversing in the same way at the dorsal ridge (vertebral area), but taking special care to follow the inclination of the lateral rows (usually 3–4) of serrated and reduced scales so as to include them in the count. Pattern cycles refers to the number of moderate to large dark markings ('saddles') on the back, starting after the first (often chevron) marking on the nape (which often extends onto the back of the head) up to the marking above the vent (in cases of bilateral asymmetry, fusion of dorsal markings, or when such dorsal markings were unclear, then lateral bars were used as guiding criteria). For specimens examined by the author, the latter four counts were usually repeated for accuracy. Scale counts on the head were taken on both sides and when different, this was indicated (see Appendix I). For the sake of calculations, in the few cases where counts were available for one side of the head only, it was considered that the counts were equivalent on the other side. Supralabials are expressed as a formula, for example, 7 [3,4], where the numbers in brackets refer to the labials (i.e., 3rd and 4th) in contact with the orbital. The most posterior labial is a large scale at the corner of the mouth.

Apart from the characters mentioned above, the following four additional features were also examined as they were found to be useful in separating the two taxa: i) Texture of the frontal scale (see usage by Bates & Broadley 2018), scored as: 0 = smooth, no pitting; 1 = a single row of pits on the posterior and lateral margins of the frontal; 2 = more extensive marginal pitting (Gans 1959: fig. 2B); 3 = extensive pitting, but with centre of frontal still smooth (Gans 1959: fig. 2A); 4 = entire frontal pitted and center of shield often rugose or corrugated. ii) Depth of the sulcus between the pair of prefrontal scales, scored as: deep or groove-like ('Y' in Appendix I), moderate ('F'), or weak with scales merely in contact ('N'), as illustrated by Gans (1959: fig. 6). iii) Relative length of prefrontal and internasal scales, determined by visual examination. iv) Protrusion of the top of the rostral scale when viewed from directly above the head, i.e., clearly visible or barely visible (only the tip of the scale is evident).

Snout-vent length (SVL; tip of snout to vent) and tail length (vent to tip of tail) were measured (usually belly-up) with the snake aligned against a millimetre ruler, but a few tightly curled specimens were measured using a length of string. Relative tail length (e.g., total length/tail length) was determined using these measurements. Measurements of truncated tails were not included in calculations.

Statistical analyses

Statistical analyses were conducted using the computer software package Statistica ver. 6. To test whether specimens assigned to the three species on the basis of their dorsal patterns ('5N' for *D. scabra*, '6N' for *D. loveridgei* and '5L' for *D. confusa*) could also be distinguished by morphological characters, a stepwise discriminant function analysis was conducted for all specimens with full sets of the relevant variables (as defined above). For

D. scabra, two specimens (JV 95149, NMWN 2287) had the '6N' pattern, and one (NMWN 9510) had a '7' (*D. palmarum*-like, see Gans 1959) pattern, whereas for *D. loveridgei* one (JV 7340) was '5N' and two (TM 33499, 49876) were intermediate (5N/6N in Appendix I); these six specimens were excluded from the analysis. Thirteen variables were analysed – meristic: numbers of ventrals; subcaudals; midbody scale rows; supralabials (for this variable and the following four, an average was used if different on either side of the head); preoculars; postoculars; anterior temporals; posterior temporals; and interval variables: frontal (scored as noted above, from 0 for smooth to 4 for extensively pitted; in a few cases where Gans [1959] had scored the frontal as 'Y' ['3/4' in Appendix I, meaning extensively pitted] a score of 3.5 was assigned, or 'N' ['1/2' in Appendix I, meaning marginally pitted] a score of 1.5 was assigned); length of prefrontal scale compared to internasal (coded as 0 if prefrontal was longest, 1 if they were equal, and 2 if the internasal was longest; score averaged if different on either side); prominence of the posterior part of the rostral when looking down on the head (0 if barely visible, 1 if clearly visible); depth of inter-prefrontal sulcus (0 if weakly marked, 1 if moderately marked and 2 if deep); and the ratio total length/tail length.

Comparative data used in diagnosis

In addition to data in this paper, comparative data for the diagnosis of *D. loveridgei* (see below) and comparison with other species was obtained from Bates (2013), Bates & Broadley (2018), Bates & Ineich (2012), Broadley (1990), Duméril et al. (1854), FitzSimons (1962), Gans (1959, 1964), Mertens (1954, 1955), Saleh & Sarhan (2016), Trape & Mané (2006), and Trape et al. (2012, 2021). For *D. atra*, to avoid inadvertently including data for mainly brown or uniform phase specimens of congeners, only data from north-east Africa (Bates & Broadley 2018) and eastern Democratic Republic of the Congo (Mount Kabobo and the 'districts' of Oriental and Kivu: Gans 1959, appendix 1) with '2M', '2B' and '2Bx' dorsal colour patterns were used. An exceptionally low female subcaudal count of 50 for *D. gansi* (see Bates & Ineich 2012), and low male ventral and subcaudal counts of 212 and 59 respectively for *D. fasciata* (see Bates & Broadley 2018), were excluded, as were high ventral and low subcaudal counts of 250 and 55 respectively for a 'male' *D. bazi* (Saleh & Sarhan 2016).

Institutional abbreviations

Material (including colour photographs) from the institutions listed below was examined. Institutional abbreviations are from Sabaj (2016).

CAS = California Academy of Sciences, San Francisco, USA
FMNH = Field Museum of Natural History, Zoology Department, Chicago, USA
JV = John Visser collection (to be accessioned into National Museum, Bloemfontein, South Africa)
MCZ = Museum of Comparative Zoology, Harvard University, Cambridge, USA
MRAC = Musée Royal de l'Afrique Centrale, Tervuren, Belgium
NHMUK = Natural History Museum, London, UK
NMW = Naturhistorisches Museum, Wien [Vienna], Austria
NMWN = National Museum of Namibia, Windhoek, Namibia
NMZB = Natural History Museum of Zimbabwe, Bulawayo, Zimbabwe
SMF = Senckenberg Naturmuseum, Frankfurt am Main, Germany
TMP = Ditsong National Museum of Natural History, Pretoria, South Africa
ZFMK = Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany
ZMB = Museum für Naturkunde, Berlin, Germany
ZMH = Zoological Museum Hamburg, Germany
ZSM = Zoologische Staatssammlung München, Munich, Germany

Species concept and species delimitation

A lineage-based species concept is followed here, where a species is represented by an independently evolving metapopulation lineage (see De Queiroz 1998, 2007; Frost & Hillis 1990). Morphological characters were the operational criteria for species delimitation.

SYSTEMATICS

Dasypeltis scabra (Linnaeus, 1758)

English: Common Egg-eater; Afrikaans: Gewone Eiervreter; German: Gewöhnlicher Eierfresser

Coluber scaber Linnaeus, 1758: 223. Type locality: 'in Indiis' [= Cape Colony, South Africa].

Dasypeltis scabra Gans 1959: 141 (part, app. 1: specimens with '5N' colour pattern, and the following specimens with '6N' pattern: FMNH 64563, 64682, 65853–4, HM 5796 [= ZMH R02271] and MCZ 39930; see Appendix I); Broadley 1983: 262 (part), 1990: 262 (part); Marais 1985: 92 (part); Branch 1988: 84 (part), 1998: 95 (part); Marais 1992: 172 (part), 2004: 270 (part), 2022: 311 (part); Schleicher 2015: 187 (part), 2018: 187 (part), 2020: 198 (part).

Dasypeltis scabra loveridgei Mertens, 1954: 213 (part, Okahandja: SMF 46371; see Discussion).

Dasypeltis scabra loveridgei (not Mertens) FitzSimons 1962: 179 (part, Tsumkwe only); ? Elzen 1980: 337 (Okaukuejo).
Dasypeltis "*scabra*" Göthel, 2015a: 19 (part).

Description. *Colour pattern* (Figs 1–2): Dorsum usually grey or light brown with dark brown to blackish markings (sometimes white-edged) in the form of saddles (41–66, mean 51.7 ± 4.83, *n* = 47) that vary in shape from square to somewhat rectangular, oval (e.g., TM 55505), irregular (e.g., CAS 196434), and often a mixture of two or more shapes; and vertically elongated markings of the same colour (sometimes white-edged) on the flanks situated between, and mostly separated from, the saddles ('5N' pattern of Gans 1959). The spaces between saddles are usually whitish and shorter (and smaller) than the saddles themselves. Occasionally the dorsal pattern is closest to '6N' (JV 95149, Katima Mulilo), or the saddles are somewhat intermediate, being squarish and only weakly constricted anteriorly and posteriorly (e.g., FMNH 65853, NMWN 2287 and ZMH R02272; also compare Figs 1–2 '*scabra*' and Fig. 8 '*loveridgei*'). Lateral markings are also variable and may be similar in this species and *D. loveridgei* (e.g., Figs 1, 9). In a few specimens some of the saddles and lateral markings are confluent, but NMWN 9510 (Waterberg) is unusual in that it has almost *D. palmarum*-like markings (colour pattern '7' of Gans 1959), with elongate to diamond-shaped saddles mostly linked to the lateral bars, forming bands. Venter white to cream, seldom immaculate (NMWN 9228, 9510; TM 22612), usually with grey stipples or dark blotches at the edges, occasionally forming a single row (TM 83351) on either side of the belly, but 2–3 well-spaced rows on either side or belly extensively marked in 84.6% (two rows on either side in 57.7%, three rows in FMNH 65854, and two rows with additional dark markings elsewhere on the belly in 23.1% – e.g., TM 39329 and 44799 which have extensively marked bellies) (*n* = 26). Top of head usually with 1–2 anterior-pointing (sometimes fragmentary) chevrons and/or other dark markings.

Scalation (Figs 3–4): Dorsal (including lateral) scales distinctly keeled; usually 3–4 (occasionally 0 or 5) rows of lateral scales keeled and serrated (*n* = 49). In most specimens, scales of the 3rd to 5th or 3rd to 6th rows from the ventral plates were serrated, but exceptions were 2nd to 6th rows (TM 55505), 3rd to 7th rows (TM 22612) and 4th to 6th rows (NMWN 9228) serrated, while juveniles NMWN 204 (202 mm SVL) and NMWN 9510 (149 mm SVL) lacked serrated laterals (*n* = 31). Preoculars usually one on either side of head, but two on either side in NMWN 4398 (*n* = 48); postoculars usually two on either side of head, but one on either side in ZMH R02272 (*n* = 48). Frontal shield heavily pitted (States 3 or 4) in 76.6% of specimens, marginally pitted (States 1 or 2) in 23.4% (*n* = 47). Inter-prefrontal suture deeply sunken in 68.1% of specimens, moderately marked in 29.8%, weakly marked in juvenile NMWN 9228 (*n* = 47). Supralabials 7 [3rd and 4th entering orbit] on either side of head in 85.7% of specimens, 6 [2,3] in 4.1%, 6 [2,3] on one side and 7 [3,4] on the other in 4.1%, and individuals with 6 [3] (NMWN 204), 7 [2,3,4] (JV 95003), and 8 [4,5] / 7 [3,4] (NMWN 4397) (*n* = 49). Temporal formula on either side of head usually 2 (anterior) + 3 (posterior) or 3+4: anterior temporals usually two on either side of head (66.7%), sometimes three (20.8%), occasionally 3 left/2 right (10.4%), and 3/4 in NMWN 7082 (*n* = 48); posterior temporals on either side of head three (54.2%), three on one side and four on the other (25.0%), four (16.7%), and individuals with two (NMWN 9510) and 3/5 (NMWN 3189a) (*n* = 48). Nasal shield usually semi-divided (i.e., suture present between nostril and first supralabial), but fully divided (suture present above and below nostril) in NMWN 4398, and undivided on left side of head and semi-divided on right in TM 39328 (*n* = 41). Prefrontal scales longer (and usually larger overall) than internasals in 90.5% of specimens, internasals longer in 4.8%, of equal length in JV 95001, and prefrontal longer on left side, equal on right, in TM 39329 (*n* = 42). When the head is viewed from above, the top of the rostral shield is visible and distinct in all but one specimen (TM 55505) in which it is barely visible (*n* = 42). Midbody scale rows 22–28 (*n* = 49), in males 22–26 (mean 24.1 ± 1.28, *n* = 15), in females 23–28 (mean 24.8 ± 1.15, *n* = 23). Ventrals 204–240 (*n* = 46), in males 204–220 (mean 210.0 ± 4.36, *n* = 15), in females 212–240 (mean 224.3 ± 6.72, *n* = 22). Subcaudals 41–62 (*n* = 45), in males 51–62 (mean 56.6 ± 3.32, *n* = 14), in females 41–55 (48.3 ± 3.61, *n* = 21).

Relative tail length: SVL/tail length in males 4.69–5.76 (mean 5.25 ± 0.38, *n* = 14), in females 5.93–8.12 (mean 7.23 ± 0.66, *n* = 19); total length/tail length in males 5.69–6.76 (mean 6.25 ± 0.38, *n* = 14), in females 6.93–9.12 (mean 8.23 ± 0.66, *n* = 19).

Size. Largest male (TMP 39329 – Katima Mulilo) 467 mm SVL + 98 mm tail length = 565 mm total length; largest female (NMWN 2292 – Witvlei, Gobabis) 730 + 97 = 827 mm, but NMWN 253 (Wilhelmsruhe) had a SVL of 773 (no tail measurement).

Localities and material examined. (Names followed by numbers refer to farms.) Breitenberg 51, Gobabis district – NMWN 2281 (2218DC); Cleveland farm, 9 km N of Otjiwarongo – TMP 83351 (2016BC); Eastern National Water Carrier, Waterberg section – NMWN 9510; Etosha Pan, Kaokoveld – FMNH 77610; Good Hope 397, Gobabis district – NMWN 2293 (2218AB); Grootfontein campground – CAS 196434 (1918CA); Grootfontein-Omatako Canal, Grootfontein district – NMWN 4924 (1917DD); Hippo 386, Gobabis district – NMWN 2290 (2219AA); Ja Dennoch, Kehoro Suid – NMWN 3189a (2318CA); Kabuta, Katima Molilo – TMP 22612 (1724DD); Katima Mulilo – NMZB–UM 24208 (1724AC); NMWN 7082, 10133 (1724AD); JV 95149, TMP 39328–9 (1724CB); Katima Mulilo, 15 km WSW

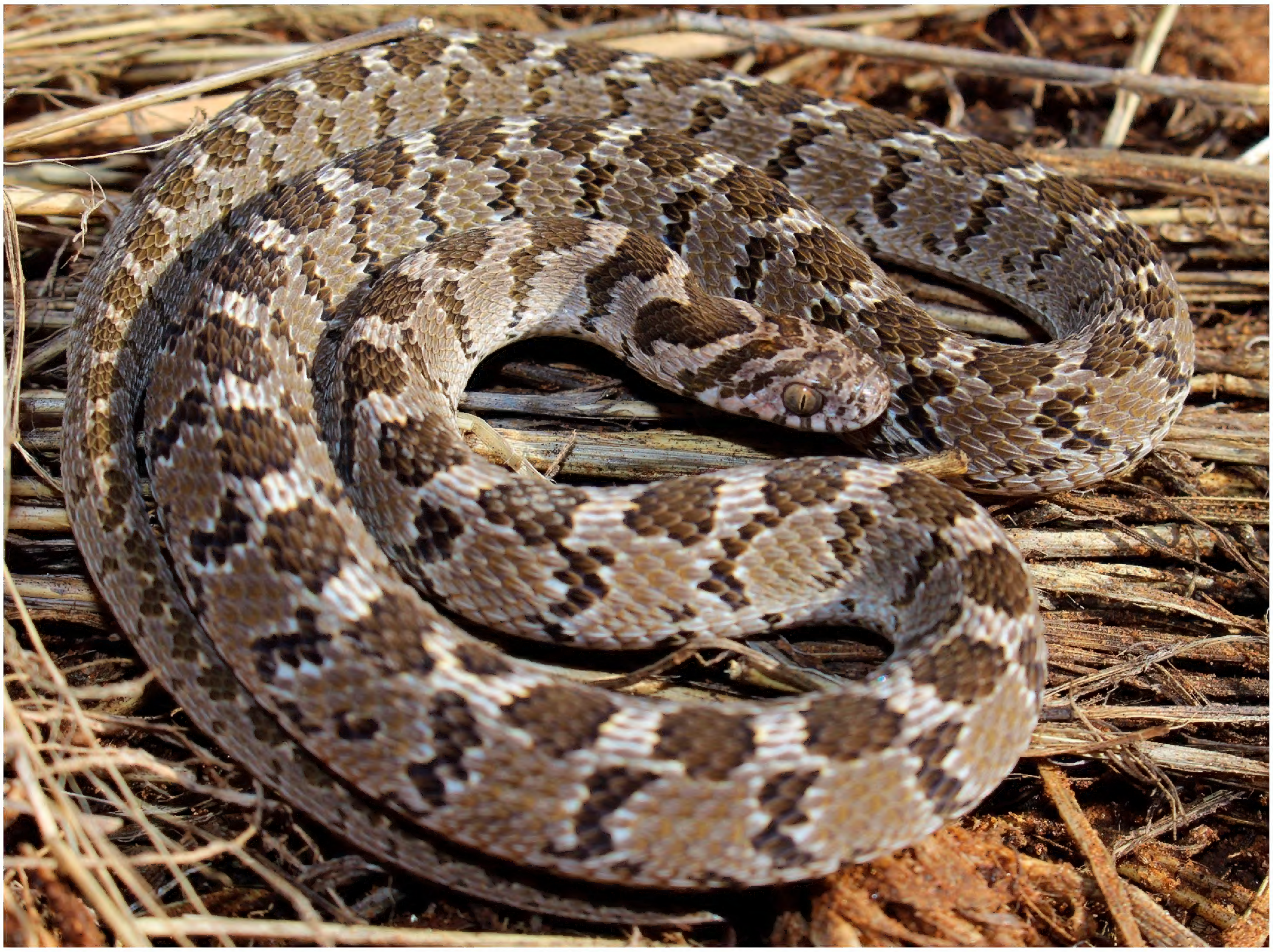

Fig. 1. *Dasypeltis scabra* from Otjiwarongo, northern Namibia. (Photo: Francois Theart)

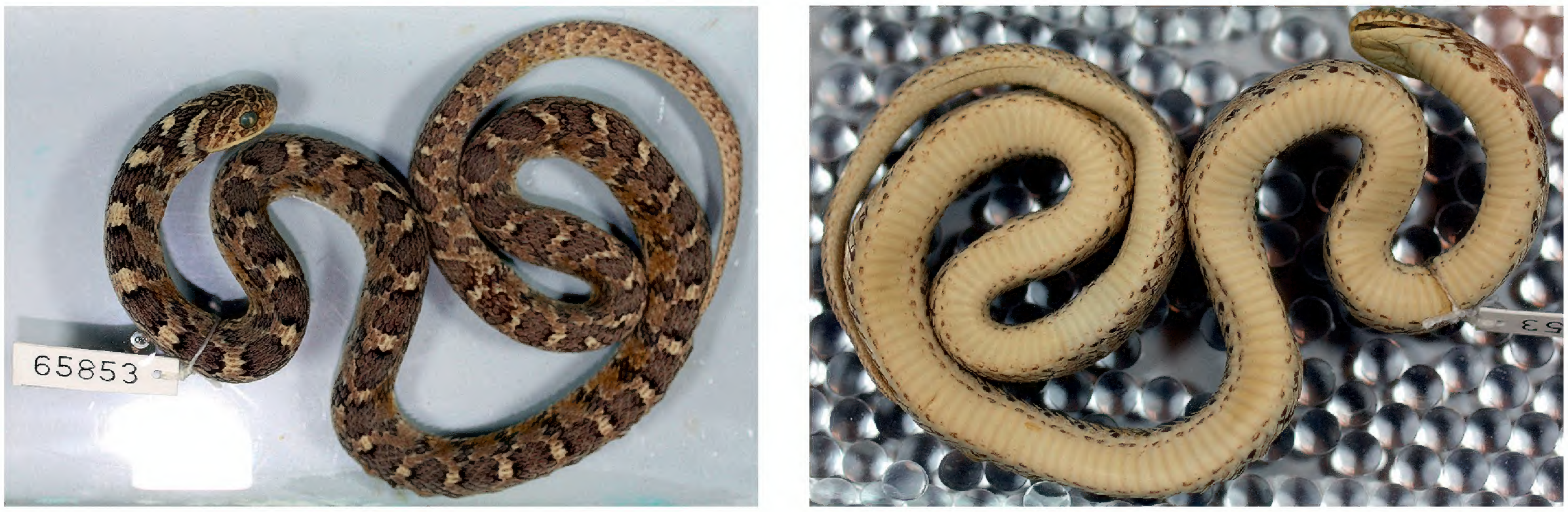

Fig. 2. Dorsal and ventral aspects of *Dasypeltis scabra* (FMNH 65853) from near Okahandja, central Namibia. (Photos: Field Museum of Natural History, Chicago)

of – NMZB–UM 22810 (1724CA); 'Namibia' – FMNH 64682, ZMB 28815; Okahandja – NMWN 204, 2294, SMF 46371, TMP 36071, ZMH R02275 (2116DD); Okahandja, near – FMNH 65853–4 (2116DD); Okahandja district – FMNH 64563; Okakena near Okahandja – ZMH R02272 (2116DD); Onjoka farm, Eastern National Water Carrier – NMWN 9228 (2017AD); Otjiwarongo – JV 95001, 95003, 95005 (2016BC); Otjosangombe – MCZ 39930 (2017AD); Outjo, 21 km due NW of – JV 8926 (2015BB); Plateau 38, Luderitz district – TMP 55505 (2616DA); Roidina farm, Omaruru district – ZMH R02271 (2116AA); Tsumkwe – NMWN

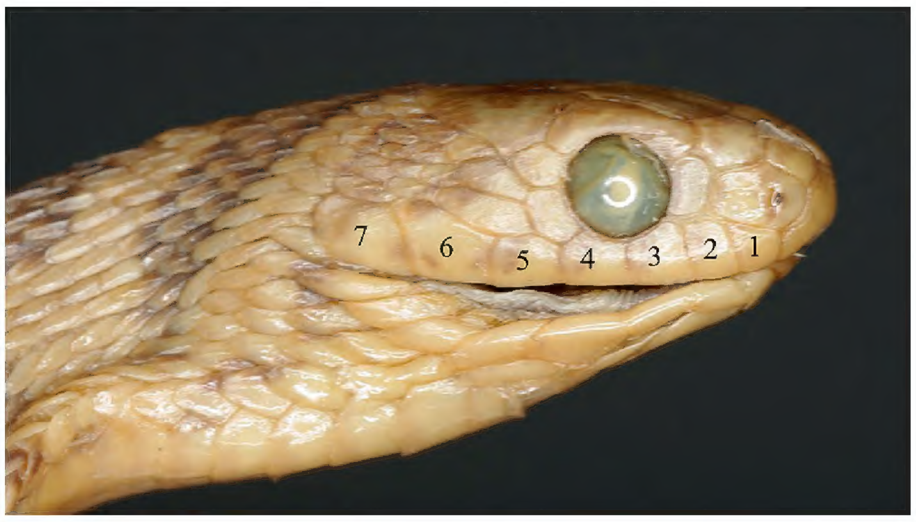

Fig. 3. Lateral aspect of the head of *Dasypeltis scabra* (SMF 46371) from Okahandja, north of Windhoek, Namibia, showing typical arrangement of seven supralabials (3rd and 4th in contact with orbital). (Photo: Sebastian Lotzkat)

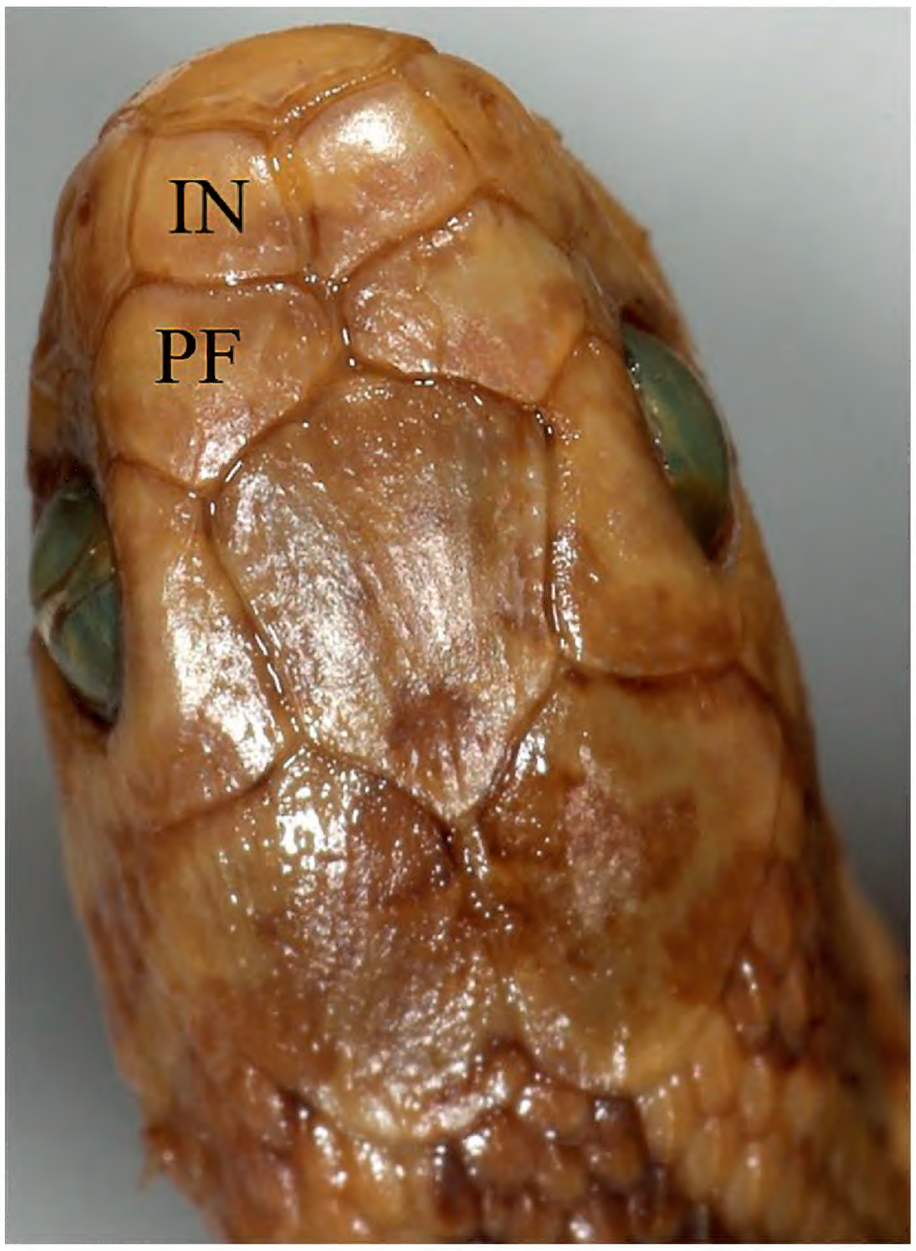

Fig. 4. Dorsal aspect of the head of *Dasypeltis scabra* (SMF 46371) from Okahandja, north of Windhoek, Namibia, showing typical condition of head shields (top of rostral shield clearly evident when viewed from above head; internasals [IN] shorter [and usually smaller overall] than prefrontals [PF]; inter-prefrontal sulcus well marked; and frontal shield extensively pitted [even partly corrugated in this case]). (Photo: Sebastian Lotzkat)

4397–8, 10131, 10135, TMP 25091 (1920DA); Waterberg Plateau – NHMUK 1937.12.3.152–3 (2017AD); Wendelstein 171, Gobabis – TMP 44799–800 (2219AC); Wilhelmsruhe 339, 45.1 km E of Steinhausen – NMWN 253 (2118DC); Windhoek – CAS 115894, NMWN 2287 (2217CA); Witvlei, Gobabis – NMWN 2292 (2118DC).

Distribution. From the south-western Cape of South Africa through Namibia, Botswana, Zambia, southern and western Democratic Republic of the Congo, much of south-eastern and eastern Africa as far north as Gojam area in north-central Ethiopia, with isolated populations along the Nile Valley in south-eastern Sudan and adjacent north-eastern South Sudan, as well as 50 km north of Kutum in western Sudan (Bates & Broadley 2018; Bates et al. 2014; Broadley 1990; Gans 1959).

In Namibia *D. scabra* is found mainly above 1000 m a.s.l., in Woodland and Shrubland-Woodland Mosaic in the north-eastern parts of the country, extending into the higher-lying central parts, with a single record in the south-west which appears to be associated with populations in the Northern Cape Province of South Africa (Fig. 5). Found in the following regions of Namibia: Kunene, Zambezi, Erongo, Otjozondjupa, Omaheke, Khomas, Hardap and Karas.

Conservation. Using IUCN (2022) criteria, this species in Namibia is considered Least Concern as it is widespread and apparently common, and there are no known major threats.

Remarks. Mertens (1955) and Gans (1959) noted that one of the paratypes (SMF 46372, Okahandja) of *D. s. loveridgei* had dorsal markings similar to those of typical *D. scabra*. One of two specimens from this locality does indeed have the '5N' pattern (and other *scabra*-like characteristics), but bears the label SMF 46371 (see Discussion).

Several specimens listed by Gans (1959) as having a '6N' dorsal pattern (hourglass-shaped markings on the back, i.e., *D. loveridgei*-like) are in fact referable to *D. scabra* (see Appendix I). Most of these specimens (FMNH 64563, 64682, 65853–4, HM 5796 [= ZMH R02271]) have a somewhat intermediate dorsal pattern in that some or most of the saddles are roughly square-shaped but moderately constricted anteriorly and posteriorly. However, other characters on these specimens were typical of *D. scabra*: supralabial formula was 7 [3,4], frontals extensively pitted, and belly had at least two rows of dark spots at the edges on either side (the latter character not recorded for the ZMH specimen). Gans (1959, appendix 1) recorded the dorsal pattern of MCZ 39930 as '?6N', but it is referable to *D. scabra* as it has the supralabial formula 7 [3,4] and an extensively pitted frontal.

Dasypeltis loveridgei Mertens, 1954

English: Namibian Egg-eater; Afrikaans: Namibiese Eirvreter; German: Namibischer Eierfresser

Dasypeltis scaber (not Linnaeus) Peters 1870 [dated 1869]: 661 (Damaraland).

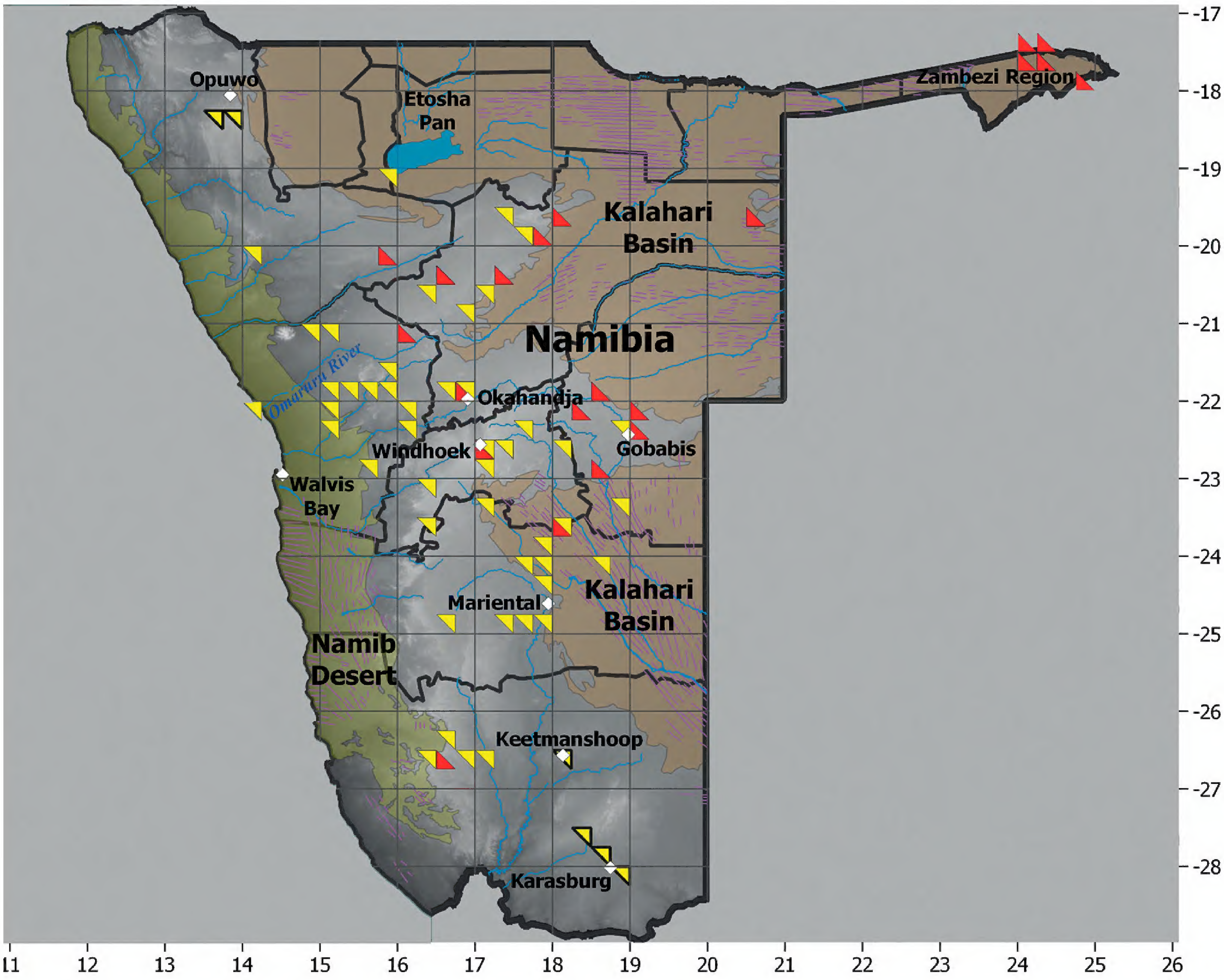

Fig. 5. Geographical distribution of egg-eating snakes (*Dasypeltis*) in Namibia, based on museum material examined for this study. Symbols represent quarter-degree grid cells (see usage in Bates et al. 2014). Red triangles = *D. scabra*, yellow triangles = *D. loveridgei*; yellow triangles with bold edges = *D.* cf. *loveridgei*. The two species are sympatric at three localities, namely Windhoek, Okahandja and Ja Dennoch (quadrants comprised of red and yellow triangles), and parapatric in several areas throughout the country.
(Map produced by Cora S Stobie using QGIS [QGIS Development Team 2020] and Natural Earth [https://naturalearthdata.com]; shapefiles for "Namibia – Kalahari and recent deserts" as well as "Biomes and vegetation types of Namibia" [Mendelsohn et al. 2002] were included for dune, river and basin data [originally available on www.the-eis.com, currently available on www.data.sasscal.org]; subnational administrative boundaries from https://data.humdata.org/dataset/cod-ab-nam; Global Multi-resolution Terrain Elevation Data 2010 [GMTED2010] [Danielson & Gesch 2011] was added to provide an elevation layer. Websites last accessed 9 Sep. 2020.)

Dasypeltis scabra (not Linnaeus) Werner 1902: 340 (Windhoek); Sternfeld 1908: 89, 1910a: 55, 1910b: 58, 1910c: 21 (Gobabis & Windhoek); Lampe 1911: 197 (Rietmond); Gans 1959: 141 (part: pl. 8, figs 3,4; pl. 5, fig. 8; and app 1: specimens with '6N' colour pattern, excluding FMNH 64563, 64682, 65853–4, HM 5796 [= ZMH R02271] and MCZ 39930, which are *D. scabra*; see Appendix I); Broadley 1983: 262 (part), 1990: 262 (part); Marais 1985: 92 (part); Branch 1988: 84 (part), 1998: 95 (part); Marais 1992: 172 (part), 2004: 270 (part), 2022: 311 (part); Schleicher 2015: 187 (part), 2018: 187 (part), 2020: 198 (part).

Dasypeltis scabra loveridgei Mertens, 1954: 213. Type locality: Farm Finkelstein near Windhoek, Namibia. Holotype: SMF 46642. (One specimen in the type series, SMF 46371, is referable to *D. scabra*; see Discussion); Mertens 1955: 104 (part, excluding 'SMF 46372' [= SMF 46371, see Discussion]); FitzSimons 1962: 179 (part, excluding Tsumkwe), 1966: 55; 1970: 114 (central highlands of Namibia), 1974: 114 (central highlands of Namibia); Elzen 1980: 337 (part, Ombujomatemba; ? Okaukuejo).

Dasypeltis loveridgei Bates et al. 2009: 69; Göthel, 2015a: 14, 19, 21 (as '*D. loverdigei*'), 2015b: 86; Bates & Broadley 2018: 6.

Dasypeltis loveridgii (sic) Marais 2022: 312 ('dry western region of southern Africa').

Revised diagnosis. Assigned to the genus *Dasypeltis* on account of its slender form; possession of (usually) 3–4 rows of reduced, oblique, keeled and serrated lateral scales (little or no serration in *D. inornata*); and head barely distinct from the neck (moderately distinct in *D. fasciata*). Distinguished from congeners by the following combination of characters: 1) Moderate to small size of males (largest: 445 mm SVL + 75 mm tail length) and females (689 + 91 mm respectively). 2) Dorsal surfaces grey, light brown or reddish-brown with a series of 36–65 dark, hourglass-shaped, patches or 'saddles'. 3) Sides of body with squarish to irregular, often vertically-oriented, dark markings (seldom distinctly elongate). 4) Ventral surfaces white to cream, immaculate or (usually) with a single row of small, often indistinct, spots or irregular markings at the edges. 5) Supralabials usually 6 on either side of head, with 2nd and 3rd in contact with the orbital. 6) Midbody scale rows longitudinally 22–25 in males, 23–27 in females. 7) Ventrals 202–226 in males, 212–236 in females. 8) Subcaudals 47–60 in males, 38–50 in females. 9) Postoculars 2 (rarely 3) on either side of head. 10) Frontal shield usually smooth to moderately pitted. 11) Inter-prefrontal sulcus almost always shallow to moderate. 12) Internasal scales usually longer (and often larger overall) than prefrontals. 13) Rostral shield barely visible from above head.

Comparison with other species. The colour pattern as described above is characteristic of *D. loveridgei*, and in this regard it differs from other species of *Dasypeltis*. While some specimens of *D. scabra* in southern Africa (e.g., Alexander & Marais 2007: 130–131; Clauss & Clauss 2002: 79) and *D. bazi* (Bates & Broadley 2018: 20) have a similar pattern, the constriction of the saddle is never as distinct and pronounced as it is in most *D. loveridgei*, and in *D. bazi* most saddles are antero-posteriorly elongated, often quite distinctly. There are 36–65 saddles in *D. loveridgei*, but in some other species this count is often much higher (108–141 in *D. fasciata*, 57–108 in *D. medici*, 65–98 in *D. abyssina*, 62–130 in patterned *D. atra*, 62–79 in *D. arabica*). Regarding the markings on the belly, in *D. loveridgei* it is immaculate or poorly marked by a single (occasionally two) longitudinal series of small dark flecks or spots at the edges of the ventral plates; whereas in *D. abyssina* it is extensively decorated in dark brown to black blotches and spots; in *D. parascabra* it is also more extensively marked, with a series of large, bold, dark markings on either side of each ventral plate, well separated from the edge, forming a pair of broken 'stripes'; in *D. medici* there are often fine grey speckles throughout; in *D. palmarum* there are usually fine dark speckles at the edges of the plates; and the underparts of *D. inornata* are usually immaculate.

Regarding scalation, the usual supralabial formula of 6 [2,3] distinguishes *D. loveridgei* from all other congeners where the formula is usually 7 [3,4] (although 6 [2,3] on both sides of the head in as much as 49.3% of *D. scabra* [*n* = 373] from Free State Province, central South Africa, based on material in the National Museum [Bloemfontein] collection; M.F. Bates, unpubl. data). Division of the nasal scale below the nostril, as in *D. loveridgei*, is the norm in the genus, but in both *D. sahelensis* and *D. parascabra* this scale is undivided. As in other species, *D. loveridgei* usually has two postocular scales on either side of the head, but specimens in western populations of *D. atra* usually have only one. The frontal shield is usually smooth to moderately pitted in *D. loveridgei* but usually extensively pitted in *D. medici* and some populations of *D. scabra*. Ventral plates in *D. loveridgei* were 202–226 in males, 212–236 in females, generally lower than in *D. arabica* (236–244 males, 239–254 females), *D. abyssina* (226–247 males, 241–271 females), *D. gansi* (221–240 males, 235–255 females), *D. medici* (220–252 males), and *D. fasciata* (225–260 females). Subcaudal counts in *D. loveridgei* were 47–60 in males, 38–50 in females, mostly lower than in *D. inornata* (81–92 males, 69–84 females), *D. fasciata* (71–91 males, 64–84 females), *D. medici* (69–109 males, 61–90 females), *D. palmarum* (68–77 males, 62–77 females), *D. gansi* (68–83 males, 59–73 females), *D. arabica* (63–65 males, 53–61 females), *D. crucifera* (61 male, 49–52 females), *D. bazi* (59–61 males, 50–55 females), *D. abyssina* (57–68 males, 49–65 females), and *D. latericia* (59–72 females).

Dasypeltis loveridgei is similar to *D. scabra* with regard to some scalation characteristics, but can be distinguished from the latter in Namibia as follows: dorsal and ventral colour patterns as described above, smaller size (largest male 445 mm SVL + 75 mm tail length versus 467 + 98 mm; largest female 689 + 91 mm versus 730 + 97 mm [one female had a SVL of 773 mm]); supralabial formula usually 6 [2,3] versus 7 [3,4]; internasal usually longer (and larger) versus shorter (and smaller) than prefrontal; frontal shield usually smooth to moderately pitted versus usually largely to extensively pitted; inter-prefrontal sulcus shallow to moderate versus usually deep and distinct; and rostral usually barely visible from above versus almost always more prominent and easily visible.

Description. *Colour pattern* (Figs 6–9): Dorsal colouration is grey, light brown or reddish-brown, with darker brown, predominantly hourglass-shaped, saddles (36–65, mean 47.3 ± 5.37, *n* = 99) constricted anteriorly and posteriorly, and usually squarish to elongated lateral markings situated between the saddles and adjacent to the pale interspaces ('6N' pattern of Gans 1959: pl. VIII fig. 4). The interspace between saddles may be as long, or longer, than the saddles themselves (e.g., Figs 6–7, 9;

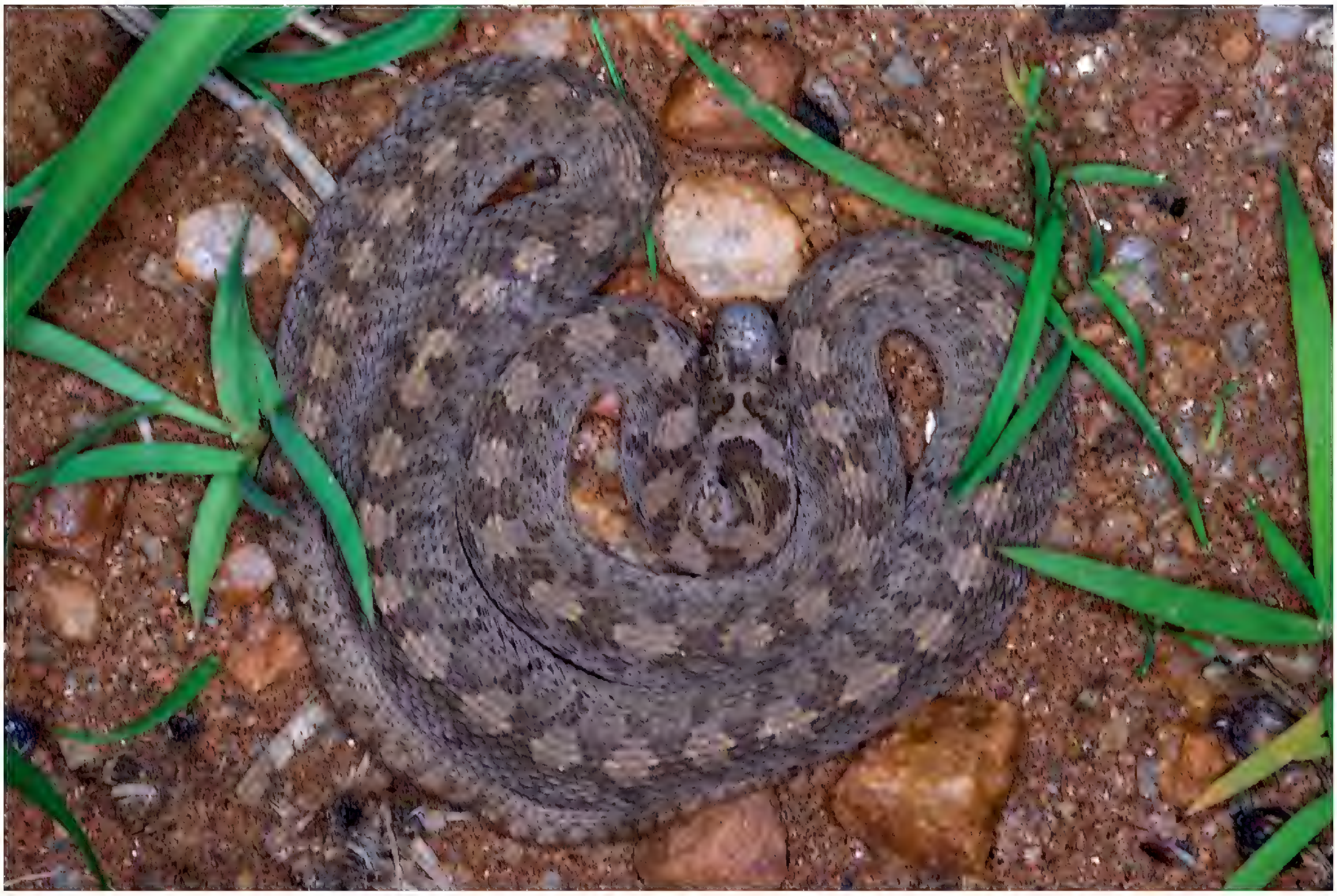

Fig. 6. *Dasypeltis loveridgei* from Dordabis, south-east of Windhoek, Namibia. (Photo: Francois Theart)

Bates & Broadley 2018: fig. 11), but occasionally much narrower (e.g., Fig. 8). Colouration and pattern in life are quite varied (Figs 6–8). For example, the snake in Fig. 6 is grey overall, with moderate sized, dark grey-brown, distinctly constricted, hourglass-shaped saddles on the back and tail, separated by cream-white interspaces that are about equal in length or slightly longer than the saddles themselves. In this specimen some saddles are greatly constricted, a few even separated into pairs of small spots paravertebrally, and the lateral markings vary from spot-like to elongate. This specimen is similar to the holotype (Fig. 9), although the latter has less strongly-constricted saddles and more elongate markings on the flanks anteriorly. The specimen in Fig. 7 has similar colouration and pattern but the saddles are large and dark brown, the interspaces between saddles are only slightly paler (whitish) than the overall grey colouration, and lateral markings are squarish to irregular in shape, seldom elongated. Figure 8 illustrates a snake with an overall light brown colour, with large, reddish-brown, weakly to moderately constricted, saddles, separated by bright white interspaces much shorter than the saddles themselves, with irregular to slightly elongated reddish-brown lateral markings (see photographs of similar snakes in Gothel 2015a: 14, 21, 2015b: 86). Other specimens with weakly constricted hourglass-shaped markings are JV 7304 (Kuibis), NMWN 2279b (Plateau 38, Luderitz), NMWN 10132 (Nauchas farm, Rehoboth), TM 48338–9 (Waterberg Plateau), and TM 42963 (Mariental). One specimen (JV 7340, near Maltahohe) had mostly the '5N' *D. scabra* pattern, while two (TM 33499 and TM 49876) had a pattern intermediate between '6N' and '5N'. Saddles and lateral markings were often fused in NMWN 6883 and NMWN 9567. Venter white to cream, immaculate in SMF 40873 and TM 29834, usually unmarked except for the edges of the plates of which some (usually at least every second ventral) have a small dark stipple or spot, usually near or at the contact point with the lateral scales, forming a weak and often poorly defined row down either side of the belly (93.9% of specimens; a few of these, including the holotype [Fig. 2], NMWN 4509 and 5299 also have fine stippling/shading at the edges of the plates), but a couple of specimens (JV 7344; NMWN 10132) have two such rows (closely spaced), while TM 29834 has only fine stippling/shading and no distinct spots/markings (*n* = 66). Top of head with (e.g., holotype, Fig. 11) or without (e.g., Fig. 8) 1–2 anterior-pointing (sometimes fragmentary) chevrons, as well as other small dark markings.

Scalation (Figs 10–11): Dorsal (including lateral) scales distinctly keeled, and usually 3–4 (occasionally 0–2) rows of lateral scales on the body keeled and ser-

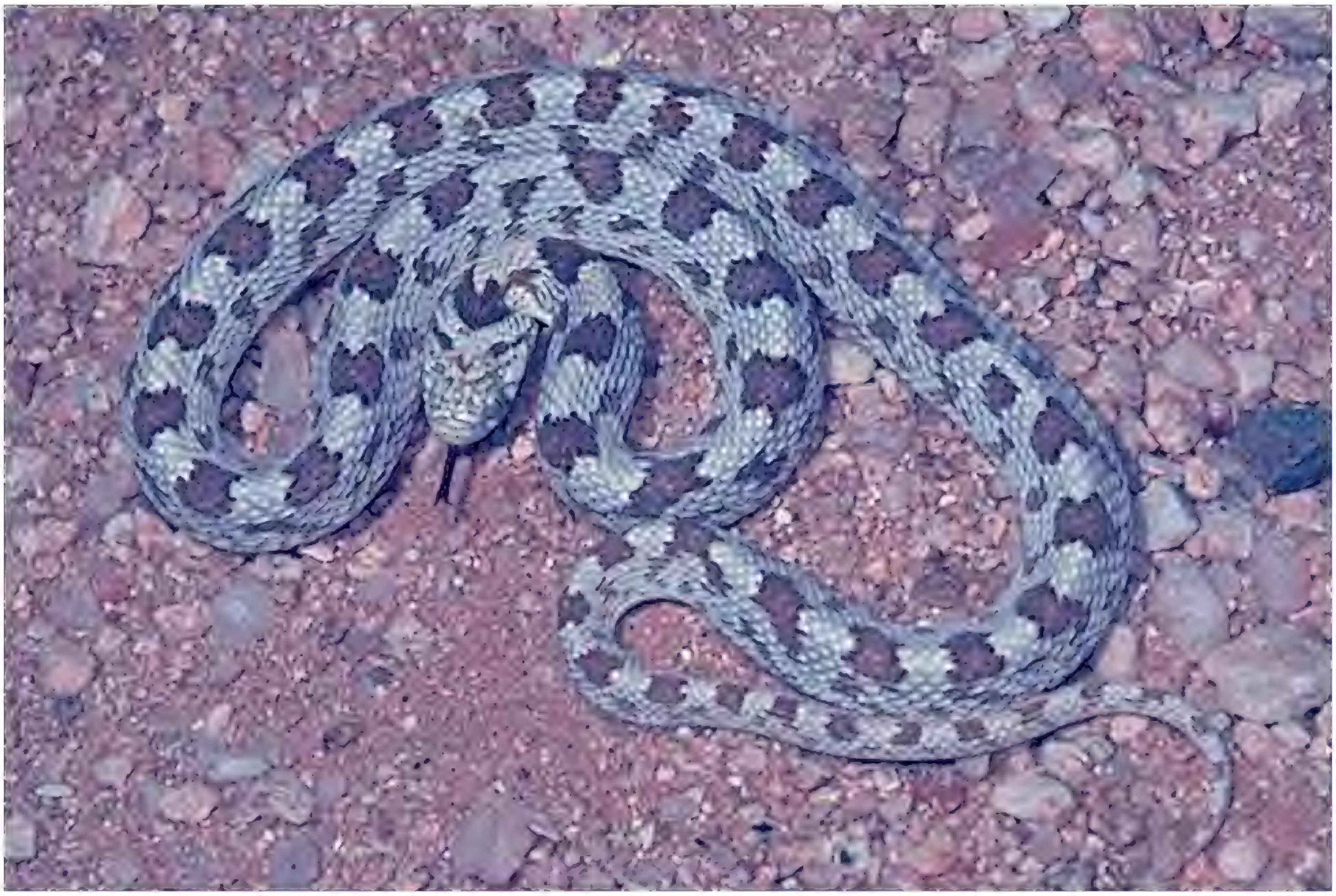

Fig. 7. *Dasypeltis loveridgei* from Klein Spitzkoppe, Erongo Region, Namibia, at the western edge of the species' range. (Photo: Wulf D. Haacke)

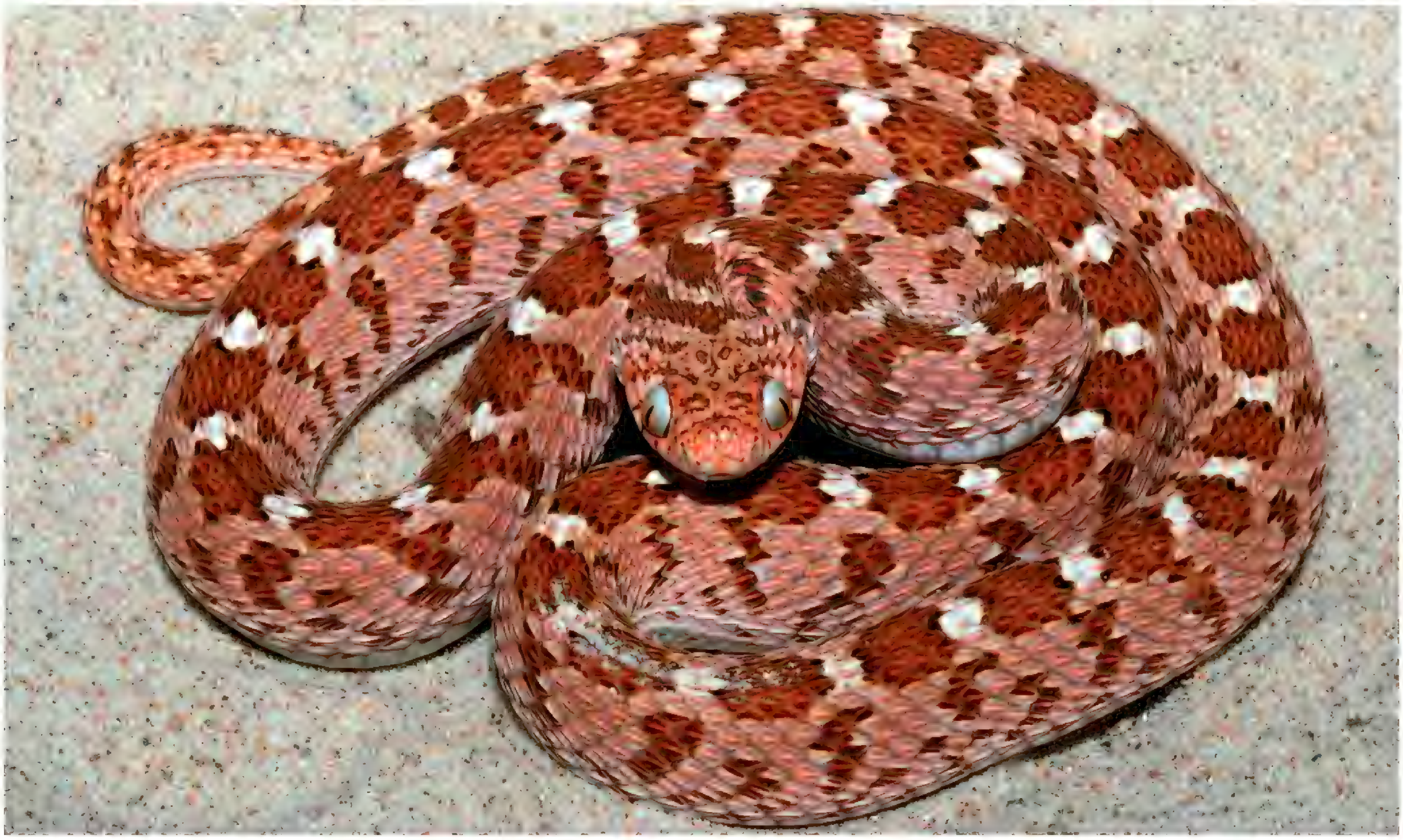

Fig. 8. *Dasypeltis loveridgei* offspring from parents collected in Tsumeb, northern Namibia. (Photo: Christian Schneider)

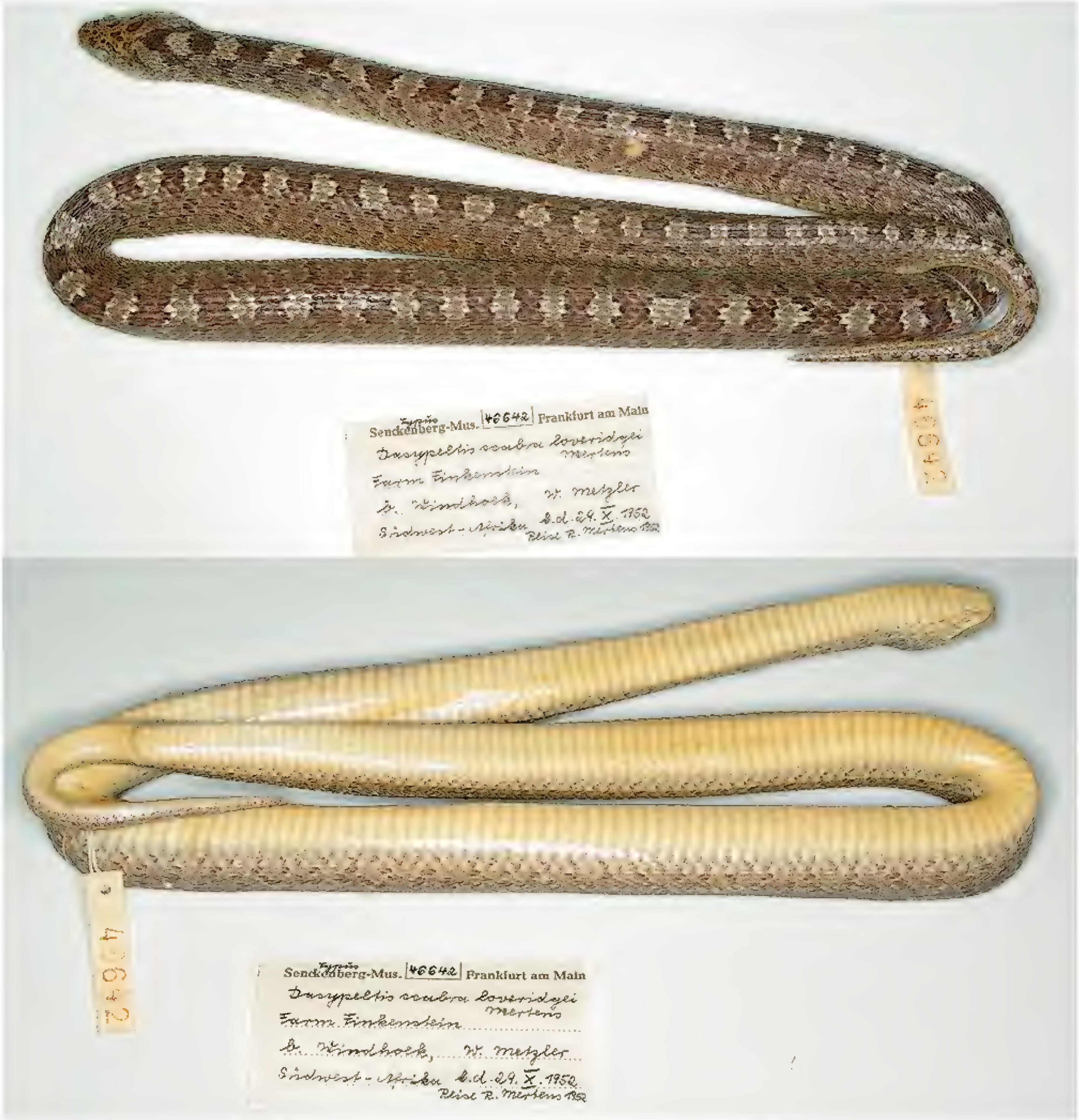
46642
Typus
Senckenberg-Mus. 46642 Frankfurt am Main
Dasypeltis scabra loveridgei Mertens
Farm Finkenstein
b. Windhoek, W. Metzler
Südwest-Afrika S.d. 29. X. 1952
Reise R. Mertens 1952
46642
Typus
Senckenberg-Mus. 46642 Frankfurt am Main
Dasypeltis scabra loveridgei Mertens
Farm Finkenstein
b. Windhoek, W. Metzler
Südwest-Afrika S.d. 29. X. 1952
Reise R. Mertens 1952

Fig. 9. Dorsal and ventral aspects of the holotype (SMF 46642) of *Dasypeltis loveridgei* Mertens, 1954 from Farm Finkenstein near Windhoek, Namibia. (Photos: Sebastian Lotzkat)

rated (*n* = 102). In most specimens, scales of the 3rd to 5th or 3rd to 6th rows from the ventral plates were serrated, but exceptions were only 4th row serrated (ZMH R02273, 208 mm SVL), 4th to 5th rows serrated (NMWN 1828, 5299), and 4th to 7th rows serrated (ZMB 33670b), while three juveniles (190–225 mm SVL: JV 7304, 8510, 8930) lacked any serrated laterals (*n* = 52). Preoculars usually one on either side of head, but two on left side and one on the right in TM 55690 (*n* = 103); postoculars usually two on either side of head, but three in NMWN 2291, and three left and two right in NMWN 1463 (*n* = 104). Frontal shield smooth in one specimen (ZMB 20920), marginally pitted (States 1 or 2) in 69.3%, and largely to heavily pitted (States 3 or 4) in 29.7% (*n* = 101). Inter-prefrontal sulcus shallow in 63.7% of specimens, moderately marked in 34.3%, and strongly marked in NMZB 10913 and SMF 41928 (*n* = 102). Supralabials 6 [2nd and 3rd contacting the orbital] on either side of head in 81.6% of specimens, 7 [3,4) in 6.8%, 7 [3,4] on one side and 6 [2,3] on the other in 7.8%, and one individual

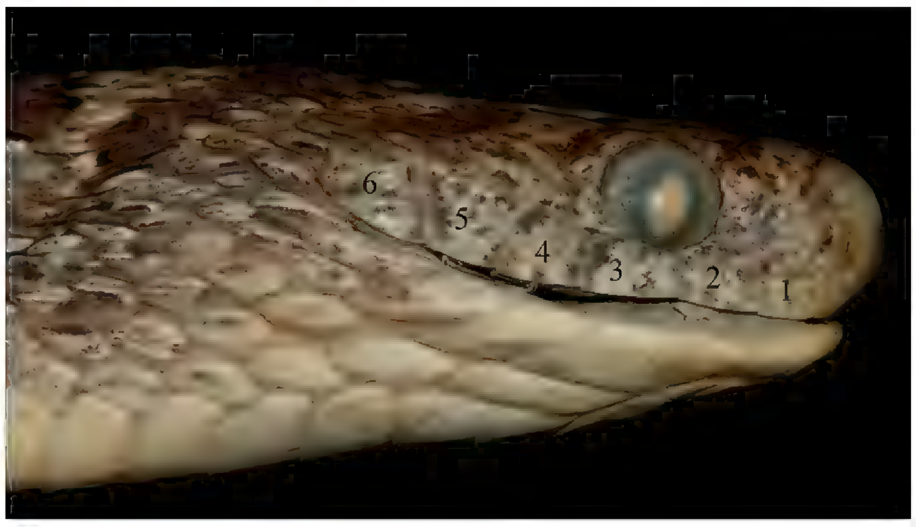

Fig. 10. Lateral aspect of the head of the holotype (SMF 46642) of *Dasypeltis loveridgei* Mertens, 1954 from Farm Finkenstein near Windhoek, Namibia, showing typical arrangement of six supralabials (2nd and 3rd in contact with orbital). (Photo: Joseph Vargas)

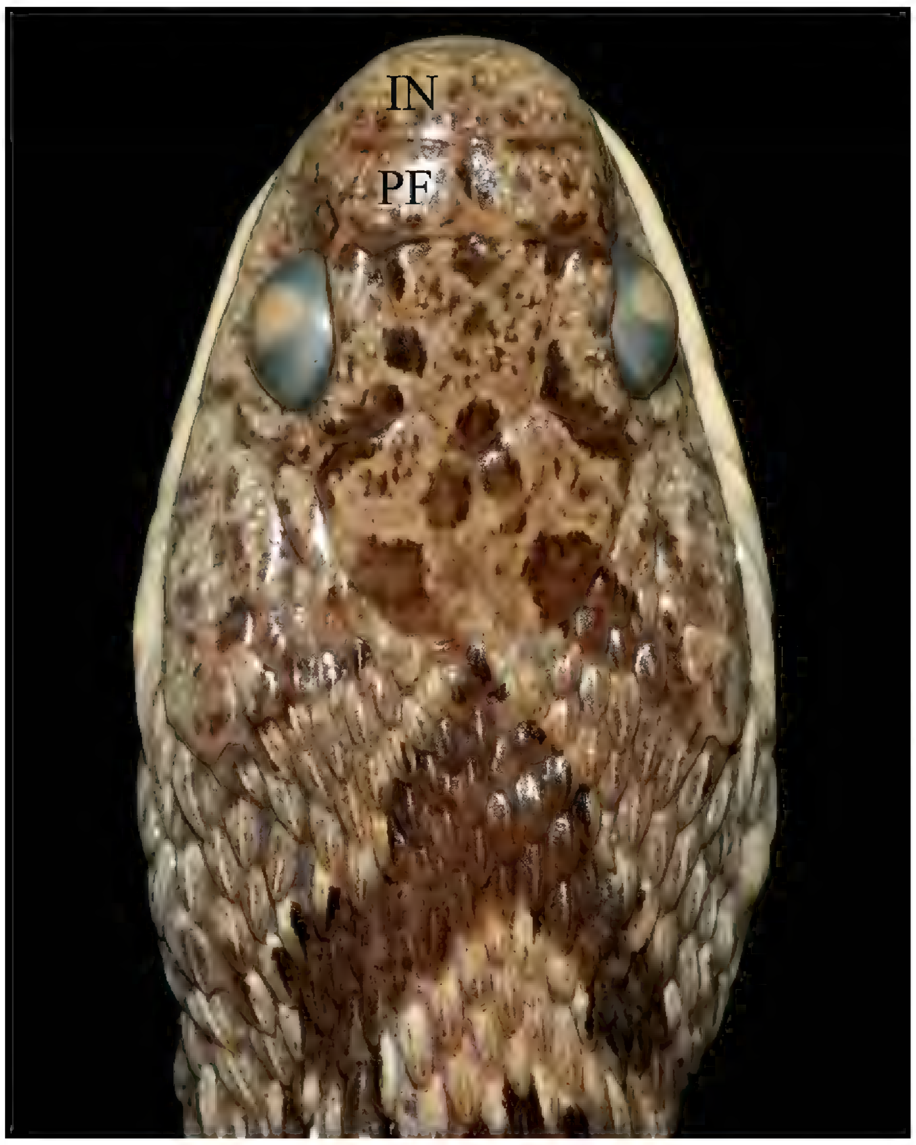

Fig. 11. Dorsal aspect of the head of the holotype (SMF 46642) of *Dasypeltis loveridgei* Mertens, 1954 from Farm Finkenstein near Windhoek, Namibia, showing typical condition of heads shields (top of rostral shield barely evident when viewed from above head; internasals [IN] longer [and often larger overall] than prefrontals [PF]; inter-prefrontal sulcus poorly marked; and frontal shield moderately pitted). (Photo: Joseph Vargas)

each with 5 [2,3] (JV 8646), 7/6 [2,3] (NMWN 2301), 7 [2,3,4] (NMWN 2303], and 7 [2,3,4] / 6 [3,4] (NMWN 235) (*n* = 103). Temporal formula on either side of head usually 2 (anterior) + 3 (posterior) or 2+4: anterior temporals usually two on either side of head (88.3%), occasionally two on one side and three on the other (6.8%), three (2.9%), one (NHMUK 1938.4.7.20), or one left and two right (NMWN 2304) (*n* = 103); posterior temporals three on either side of head (53.4%), 3/4 (20.4%), four (17.5%), four on the one side and five on the other (5.8%), 5/3 (NMWN 1463), 3/2 (NMWN 2288b), and two (ZMB 20983) (*n* =103). Nasal shield semi-divided (i.e., suture present between nostril and first supralabial) in 90.5% of specimens, entirely undivided in 3.2% (e.g., TM 28147), semi-divided on one side of the head and undivided on the other in 3.2%, semi-divided on one side and fully divided (suture above and below nostril) on the other in ZMB 20983, fully divided on both sides of the head in ZMB 20984, and undivided on the left and fragmentary on the right in NMWN 9585b (*n* = 95). Internasal scales longer (and often larger overall) than prefrontals in 58.9% of specimens, equal in length in 25.6%, longer than prefrontal on one side and equal on the other in 2.2%, prefrontals longer in 12.2%, prefrontal longer on the left and shorter on the right in NMWN 2288b (*n* = 90). When the head is viewed from above, the top of the rostral shield is barely visible in 93.1% of specimens, but distinct in 6.9% (*n* = 87). Midbody scale rows 22–27 (*n* = 101), in males 22–25 (mean 23.4 ± 0.78, *n* = 39), in females 23–27 (mean 24.2 ± 0.97, *n* = 35). Ventrals 202–237 (*n* = 102), in males 202–226 (mean 214.3 ± 5.38, *n* = 40), in females 212–236 (mean 225.7 ± 6.25, *n* = 36). Subcaudals 38–60 (*n* = 100), 47–60 in males (mean 52.7 ± 3.00, *n* = 41), 38–50 in females (mean 45.2 ± 2.80, *n* = 34).

Relative tail length: SVL/tail length in males 4.74–7.10 (mean 5.89 ± 0.54, *n* = 38), in females 6.33–9.26 (mean 7.42 ± 0.55, *n* = 35); total length/tail length in males 5.74–8.10 (mean 6.89 ± 0.54, *n* = 38), in females 7.33–10.26 (mean 8.42 ± 0.55, *n* = 35).

Size. Largest male (ZMB 5754 – Otjimbingwe) 445 + 75 = 520 mm; largest female (JV 8646 – Uis) 689 + 91 = 780 mm.

Localities and material examined. Between Arandis and Usakos – JV 8510; Augustfelde 42, Luderitz district – TMP 52749 (2616CB); De Waal farm – TMP 28147 (2318BD); Finkenstein farm, Windhoek – NMWN 2278, 2304, SMF 46642 (2217CB); Gemsbokwater, Namib Naukluft Park – TMP 55690 (2215DC); Goageb, 2 km W of – JV 7338 (2617CA); Gobabis – ZMB 20923, 20983–4, 20858a–b (2218BD); Haribes NW 18, near Gibeon – NMWN 2277 (2417DC); Ja Dennoch, Kehoro Suid – NMWN 3189c (2318CA); Kalkrand, Rehoboth – NMWN 2282, 2291 (2417BA); Karibib – NMWN 2297–8 (2115DD); Karibib, 42.3 km W of, on B2 route – JV 7448 (2115CD); Klein Spitzkoppe 70, Karibib district – TMP 42300 (2115CC); Klein Windhoek – SMF 19446 (2217CA); Kuibis, 5.5 km due NW of – JV 7304 (2616DB); Lichtenstein farm near Windhoek – ZMB 44052, ZMH R02273 (2217CA), ZMB 27648 (2217CC); Maltahohe, 37 km due W of – JV 7344 (2416DC); Mariental, 30 km S of – TMP 49876 (2417DD); Mariental–Rehoboth – NMZB 10913; M'bela 200, Rehoboth – NMWN 2300, 2302–3 (2317DD); 'Namibia' – FMNH 57654, ZMB 21530; Nauchas farm, Rehoboth Gebied – NMWN 10132 (2316CB); Neudamm, E of Windhoek – NMWN 2296 (2217CB); Nunib farm, E of Stampriet – TMP 30499 (2418BA); Okahandja – FMNH 64487, NHMUK 1938.4.7.20, NMWN 2289, SMF 46372, TMP 39515 (2116DD); Okahandja, 19 km N of, on B1 route – NMWN 6883 (2116DD); Okanjati farm, Kalkveld – NMW 9963–3 [one specimen] (2016CB); Okapehwu farm near Okasise, Okahandja district – ZMH R02274 (2116DC); Okasise, Okahandja – TMP 29834 (2116DD); Okaukuejo Camp, Etosha National Park – NMWN 9585a–b (1915BB); Okosongomingo 149, Otjwarengo district – NMWN 6828a (2017CA); Omaruru River – TMP 33499 (2214AA); Omaruru, 17.5 km S of, on C33 route – JV 7446 (2115DB); Otjimbingwe – ZMB 5754, 33670a–b (2216AC); Otjozondu 36, Karibib district – NMWN 8255 (2216AA); Paulienenhof farm – ZMH R02289 (2217CB); Plateau 38, Luderitz district – NMWN 2279a–b (2616BC), TMP 48337–9 (2616CB); Rehoboth – NMWN 2280 (2317AC); Rentes 783 – NMWN 235 (1917CB); Scheidthof 293, Windhoek district – NMWN 1828 (2218CA); Seeis, Windhoek district – TMP 58046, ZMH R02270 (2217BC); Springbok Gate, Skeleton Coast National Park – NMWN 7791 (2014AA); Sukses – SMF 46373 (2016DD); Swakopmund, 77 km due NE of – JV 7405 (2215AC); Swakopmund, 90 km NE of, on B2 route – JV 8930 (2215AA); Swakopmund, 96 km due NE of – JV 7407 (2215AA); Twilight 113, Mariental district – NMWN 2305, TMP 42963 (2417BB), NMWN 1463 (2417BD); Uis – JV 8646 (2114BB); Uis Mine, Omaruru district – TMP 54333 (2114BB); Usakos, Karibib – TMP 25810–1 (2115DC); Usakos, near – MRAC 94-041-R-0002 (2115AA); Valencia 42, Rehoboth – NMWN 2288a–b, TMP 35605 (2316AB); Voigtsgrund farm, 49 km due E of Maltahohe – JV 7340 (2417CD); Windhoek – NMWN 2283–6, 2295, 2299, 2301, 3429, SMF 40873, 41928, 46370, 49617, ZMB 20920, 20982 (2217CA); Windhoek, Mandume Ndemufayo Avenue [Gamsberg Road] – NMW 35792 (2217CA); Windhoek, Olympia suburb – NMWN 4509 (2217CA); Windhoek, Pioneers Park – NMWN 238 (2217CA); Windhoek, 0.1 km past steel bridge [Avis] – NMWN 9567 (2217CA); Windhoek, 14 km E of – NMWN 9208 (2217CA); Windhoek and Okahandja, between – ZMB 20921; Zabis 153, Grootfontein district – NMWN 5299 (1917DC).

Dasypeltis cf. *loveridgei*: Kaoko Otavi – NMWN 1465 (1813BC); Karasburg, 5 km NNW of – TMP 54997 (2718DC); Karasburg, 11 km due ENE of – JV 7317 (2818BB); Keetmanshoop, W of – CAS 173379 (2618CA); Mickburg farm, NNE of Grunau – TMP 54996 (2718CB); Orumana, Ohopoho – NMWN 2306 (1813BD).

Distribution. Widespread in Namibia, especially in areas above 1000 m a.s.l., but excluded from the Namib Desert in the west of the country, as well as Woodland and most of the Shrubland-Woodland Mosaic in the north-eastern parts of the country (Fig. 5). Found in the following regions of Namibia: Kunene, Oshikoto, Erongo, Otjozondjupa, Omaheke, Khomas, Hardap, and Karas.

Sympatric with *D. scabra* at the following localities: Windhoek (2217CA), Okahandja (2116DD) and Ja Dennoch (2318CA), and parapatric in several areas throughout the country. The two species also occur together at Etosha Pan (*D. loveridgei*: Okaukuejo camp, *D. scabra*: 'Etosha Pan'), but the locality details for *D. scabra* are too course to plot in Fig. 5.

Conservation. Using IUCN (2022) criteria, this species is considered Least Concern as it is widespread and apparently common, and there are no known major threats to it.

Remarks. FitzSimons' (1962) record of a 'Transvaal Museum' specimen of *D. s. loveridgei* from Tsumkwe in north-eastern Namibia (plotted at 1920BC on his map 32, p. 178), probably in reference to TMP 25091, is referable to *D. scabra*. This specimen and four others from the same locality (see Appendix I) had the typical '5N' *D. scabra* dorsal colour pattern and supralabial formula of 7 [3,4] (but 8 [4,5] on the right side in NMWN 4397).

Photographs of Elzen's (1980) ZFMK 5426 from Ombujomatemba (Jagd Farm), south of the Waterberg range, were examined and confirm that the specimen is a *D. loveridgei* (weakly constricted hourglass-shaped saddles on back; supralabial formula 5 [2,3] left, 6 [2,3] right; frontal marginally pitted). Elzen (1980) also recorded *D. s. loveridgei* from Okaukuejo (camp) in Etosha National Park, but did not provide a photograph or other evidence (it is not in the ZFMK collection according to M. Flecks, pers. comm., July 2022); and this is an area where both *D. scabra* and *D. loveridgei* may occur (see Fig. 5).

Göthel (2015b) did not provide supporting data for his contention that *D. loveridgei* differs from other *Dasypeltis* by the fine markings on its head. Marais (2022) noted that *D. loveridgei* can be distinguished from *D. scabra* only by having six upper labials, and red colouration. He failed to mention any differences in dorsal markings (e.g., '5N' versus '6N') and *D. loveridgei* is not always 'red' (or even reddish-brown).

Key to the genus *Dasypeltis* in Namibia

Dorsal markings in the form of dark brown squarish, rectangular, oval or irregular saddles; belly usually with at least two rows of dark markings on sides; usually 7 supralabials (3rd and 4th contacting orbital); prefrontals usually longer (and larger overall) than internasals; top of rostral clearly visible when head is viewed from above; frontal usually largely to extensively pitted; inter-prefrontal sulcus moderate or (usually) deep .. *D. scabra*

Dorsal markings in the form of dark brown to reddish-brown hourglass-shaped saddles (deeply to moderately constricted anteriorly and posteriorly); belly usually with single row of small dark markings at edges; usually 6 supralabials (2nd and 3rd contacting the orbital); prefrontals usually shorter (and often smaller overall) than internasals; top of rostral usually barely visible when head is viewed from above; frontal usually smooth to moderately pitted; inter-prefrontal sulcus weakly marked or moderate .... *D. loveridgei*

MULTIVARIATE ANALYSIS

A total of 110 specimens (30 *D. scabra*: 10 males, 14 females, 6 unsexed; 72 *D. loveridgei*: 24 males, 31 females, 17 unsexed; eight *D. confusa*: at least one male, but ZMH R08914 is probably also a male based on its low ventral and high subcaudal counts, and six females) had complete sets of data and were used in the discriminant function analysis. Three variables (postoculars, anterior temporals, posterior temporals) of the 13 exhibited little variation and were excluded from the model. In the analysis, 98.2% of specimens were correctly classified, including all *D. confusa*, 96.7% of *D. scabra* and 98.6% of *D. loveridgei* (Table 1). The only specimen of *D. loveridgei* misclassified (as *D. scabra*) was NMWN 9567, which unusually had the prefrontals longer than the internasals and the rostral distinctly visible from above; while one specimen (NMWN 9228) of *D. scabra* atypically had a marginally pitted frontal (State 1) and a weak inter-prefrontal sulcus and was misclassified as a *D. confusa*. *Dasypeltis loveridgei* was for the most part distinguished from *D. scabra* and *D. confusa* along axis 1, on which number of subcaudals (-0.93), the ratio total length/tail length (-0.83), prominence of the rostral scale (-0.67) and number of sublabials (-0.57) loaded most heavily; while *D. loveridgei* and *D. scabra* were for the most part distinguished from *D. confusa* along axis 2, on which subcaudals (1.51), total length/tail length (0.89) and depth of inter-prefrontal sulcus (-0.51) loaded most heavily (Fig. 12, Table 2).

Table 1. Observed (rows) and predicted (columns) classifications of *Dasypeltis* (*D. scabra*, *D. loveridgei*) from Namibia and *D. confusa* from Angola and south-western Democratic Republic of the Congo according to the discriminant function analysis.

	% correct	***D. scabra***	***D. loveridgei***	***D. confusa***
		0.273	**0.655**	**0.073**
Dasypeltis scabra	96.7	29	0	1
Dasypeltis loveridgei	98.6	1	71	0
Dasypeltis confusa	100	0	0	8
Total	98.2	30	71	9

Table 2. Standardised coefficients for canonical variables in the discriminant function analysis of *Dasypeltis* (*D. scabra*, *D. loveridgei*) from Namibia and *D. confusa* from Angola and south-western Democratic Republic of the Congo.

	Function 1	**Function 2**
rostral	-0.666154	-0.019163
inter-prefrontal sulcus	-0.234152	-0.508741
sublabials	-0.572065	0.020463
subcaudals	-0.928391	1.509666
total length/tail length	-0.829819	0.891548
internasal/prefrontal	0.364874	0.166350
midbody scale rows	-0.268441	0.083595
preoculars	0.024294	0.343310
ventrals	0.156361	0.321922
frontal	-0.031251	-0.200775
eigenvalue	9.600167	1.322523
cumulative proportion	0.878920	1.000000

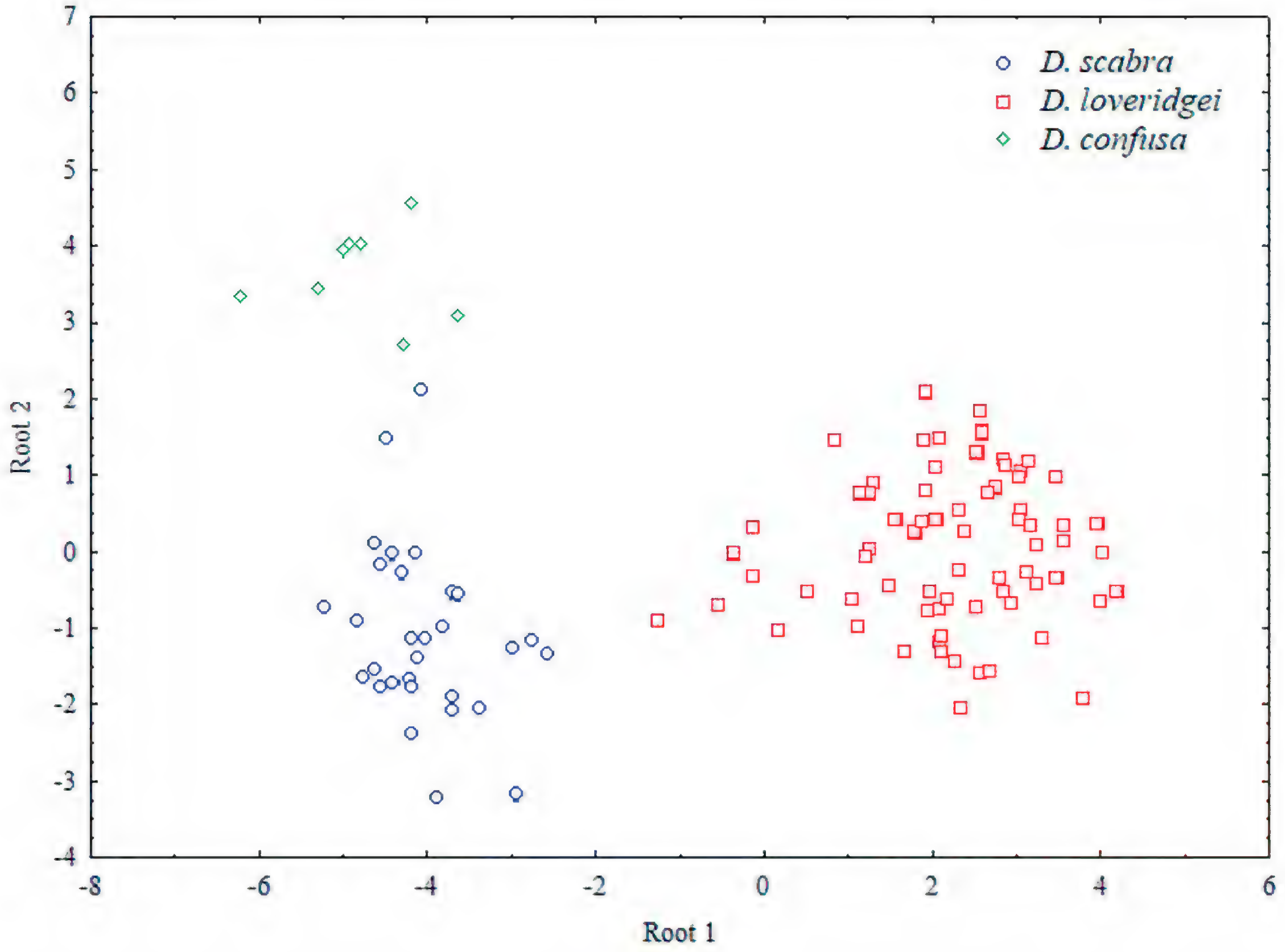

Fig. 12. Discriminant function analysis of *Dasypeltis scabra* and *D. loveridgei* from Namibia, and *D. confusa* from Angola and south-western Democratic Republic of the Congo.

DISCUSSION

Mertens' (1954) description of *D. s. loveridgei* provided only two supposedly diagnostic characters, namely the possession of hourglass-like markings on the back, and a suggestion that the new taxon had greater numbers of ventral plates than typical *D. scabra*. In *D. loveridgei* the saddles are in the form of an hourglass, often with the interspace between saddles similar in size to the saddles themselves, whereas in *D. scabra* the saddles are square, rectangular, oval, and/or a variety of other, often irregular, shapes, and the interspaces between them are usually smaller than the saddles themselves. Also, in Namibian *D. scabra* the colour is never reddish-brown as in some populations of *D. loveridgei* (e.g., Fig. 8).

Gans (1959) noted that Mertens (1954) had essentially named a new subspecies on the basis of its dorsal pattern. Although he treated *D. s. loveridgei* as a synonym of *D. scabra*, Gans (1959) did in fact recognise its unique dorsal pattern, naming it '6N'. He listed several Namibian *Dasypeltis* specimens that fitted the '6N' pattern, and noted (p. 117) that: "There is a reduction in the frequency of [the supralabial formula] 6(2,3) proceeding northward within southwest Africa, with the three specimens [actually two] from the Waterberg plateau and the Mossamedes [SW Angola] record having 7(3,4) pattern." Gans (1959, appendix 1) listed 33 specimens of Namibian *Dasypeltis* with positive data for numbers of supralabials as well as dorsal colour pattern. Of these, only 10 snakes (from at least five localities) had the supralabial formula 7 [3,4] on at least one side (usually both sides) of the head, and of these, three also had the '5N' dorsal pattern (i.e., *D. scabra*). Instead of looking for a correlation between dorsal colour pattern and supralabial formula, Gans (1959) appears to have simply analysed all Namibian *Dasypeltis* together. Had he excluded the specimens with '5N' patterns, the correlation between '6N' dorsal pattern and 6 [2,3] supralabial formula (i.e., indicative of *D. loveridgei*) would have been more evident (see below).

FitzSimons (1962) later recorded *D. s. loveridgei* from Namibia and noted that its colour pattern (shape of saddles and lateral markings) differed markedly from *D. s. scabra*. Although he emphasised that *D. s. loveridgei* had lower numbers of dorsal saddles (42–54), the present study indicated that there is considerable overlap in this character between the two species and it does not appear to be diagnostic (36–65, mean 47.3, in *D. loveridgei* versus 41–66, mean 51.7, in *D. scabra*). Broadley (1983, 1990), using a larger sample, subsequently noted a lack of correlation between dorsal colour pattern and characters such as supralabials, ventrals and subcaudals.

However, the present study determined that there was indeed a strong correlation between colour pattern and supralabial formula in both morphotypes. In *D. scabra* 85.4% of the sample (*n* = 48) had the typical *D. scabra* dorsal pattern ('5N') of dark oval, squarish, rectangular or irregular-shaped saddles usually with elongate lateral markings, as well as the supralabial formula 7 [3,4] on at least one side of the head (91.8% [*n* = 49] had the typical *D. scabra* dorsal pattern, and 91.8% [*n* = 49] had the supralabial formula 7 [3,4] on at least one side), whereas in *D. loveridgei* 87.4% (*n* = 103) had the typical *D. loveridgei* dorsal pattern ('6N') of hourglass-shaped saddles usually with squarish to irregular lateral markings, as well as the supralabial formula 6 [2,3] on at least one side of the head (97.1% [*n* = 104] had the typical *D. loveridgei* dorsal pattern, and 90.3% [*n* = 103] had the supralabial formula 6 [2,3] on at least one side). In a few cases the colour pattern assigned to a specimen did not match its species assignment ('5N' for *D. scabra* and '6N' for *D. loveridgei*). For example, JV 95149 is considered *D. scabra* although it has a weakly '6N'-like pattern, but for this specimen and other such cases, the majority of morphological characters were *D. scabra*-like. The same applied to specimens of *D. loveridgei* with '5N' or intermediate ('5N/6N') patterns.

Regarding colour pattern, it has been suggested that *D. loveridgei* is a mimic of the horned adder *Bitis caudalis* (A. Smith, 1839), a thick-bodied viperid snake with a similar dorsal pattern (Branch 1998; Broadley 1983, 1990; Dobiey & Vogel 2007; FitzSimons 1962; Mertens 1954, 1955; Sternfeld 1908, 1910a-c; Werner 1902). In Namibia the distribution ranges of these two species overlap almost entirely (see Fig. 5 for *D. loveridgei*, and maps on p. 116 in Branch 1998 and p. 110 of Dobiey & Vogel 2007 for *B. caudalis*). The resemblance in dorsal markings between the two species, which also both have strongly keeled dorsal scales, can be quite remarkable (e.g., Branch 1998: pl. 13 figs 1, 3; Clauss & Clauss 2002: 89). Both *D. loveridgei* and the horned adder are absent from the north-eastern parts of the country where only *D. scabra* occurs; and the species that the latter has been said to mimic, the common night adder *Causus rhombeatus* (Lichtenstein, 1823), occurs in the vicinity of the Caprivi in the north-east of Namibia (see Fig. 5; and maps in Branch 1998, Broadley 1990 and Dobiey & Vogel 2007).

Two of Mertens' (1954) paratypes of *D. s. loveridgei* were listed as follows: "♂♀ Senck. Mus. Nr. 46371-72. Okahandja, Südwesafrika; W. Hoesch 1.1952." In his monograph on the amphibians and reptiles of South West Africa, Mertens (1955) noted that one of the *D. s. loveridgei* paratypes (SMF 46372, female, Okahandja) had dorsal markings more similar to those of typical *D. scabra*, leading him to wonder whether its locality information was correct. It can be confirmed that one of the paratypes, a female, shown in Fig. 13 where it bears the label SMF 46371, does indeed have the '5N' dorsal pattern, as well as other features typical of *D. scabra* such as the supralabial formula 7 [3,4], prefrontals longer than internasals, rostral clearly visible from above, and two rows of dark spots at the edges of the venter. This is clearly the same specimen referred to by Mertens (1954, 1955) and Gans (1959) as SMF 46372. The two specimens were collected at Okahandja and their details were recorded on the same label (Fig. 13) at the Senckenberg Museum, Frankfort. Confusion as to which specimen was which may have resulted if the specimens did not previously have individual labels, but it could also be due to the labels being inadvertently switched, presumably after 1959. Several specimens of both species have in fact been collected in and around Okahandja in central Namibia (see lists of localities), and the two species also occur sympatrically at two other localities in that general area, namely Windhoek and Ja Dennoch, and parapatrically in several additional areas throughout the country (Fig. 5). Surprisingly, although *D. scabra* is quite widespread in the east of Namibia and in the Caprivi region, it was not recorded from the country by Mertens (1954, 1955).

The present study also confirms differences in ventral colour pattern. FitzSimons (1962) had referred to the 'uniformly' white underparts of *D. loveridgei* versus underparts with dark markings, especially at the edges, in *D. scabra*. Close inspection indicated that in 97.0% (*n* = 66) of *D. loveridgei* there are actually small dark markings on the lateral edges of at least some ventrals, forming vague rows (usually one) on either side of the belly, while in comparison, *D. scabra* usually has more extensive dark markings including, in most cases, at least two rows on either side of the belly. While as much as 97.0% (*n* = 66) of the *D. loveridgei* sample had immaculate or weakly marked (single row of dark markings at the extreme edges) bellies, as much as 84.6% (*n* = 26) of *D. scabra* had well marked bellies (two or three rows of dark markings on either side, sometimes with additional scattered dark markings elsewhere on the belly).

FitzSimons (1962) had suggested that *D. s. loveridgei* was smaller than the typical form, growing to 663 mm in total length (585 mm snout-to-vent + 78 mm tail), and later stated that it did not exceed 75 cm in (total) length (FitzSimons 1974). A larger female specimen (689 + 91 = 780 mm) of *D. loveridgei* was examined in this study, but this is still smaller than the largest Namibian *D. scabra*, a female measuring 730 + 97 = 827 mm (another female had a SVL of 773 mm). The largest males in the present study measured 445 + 75 = 520 mm (*D. loveridgei*)

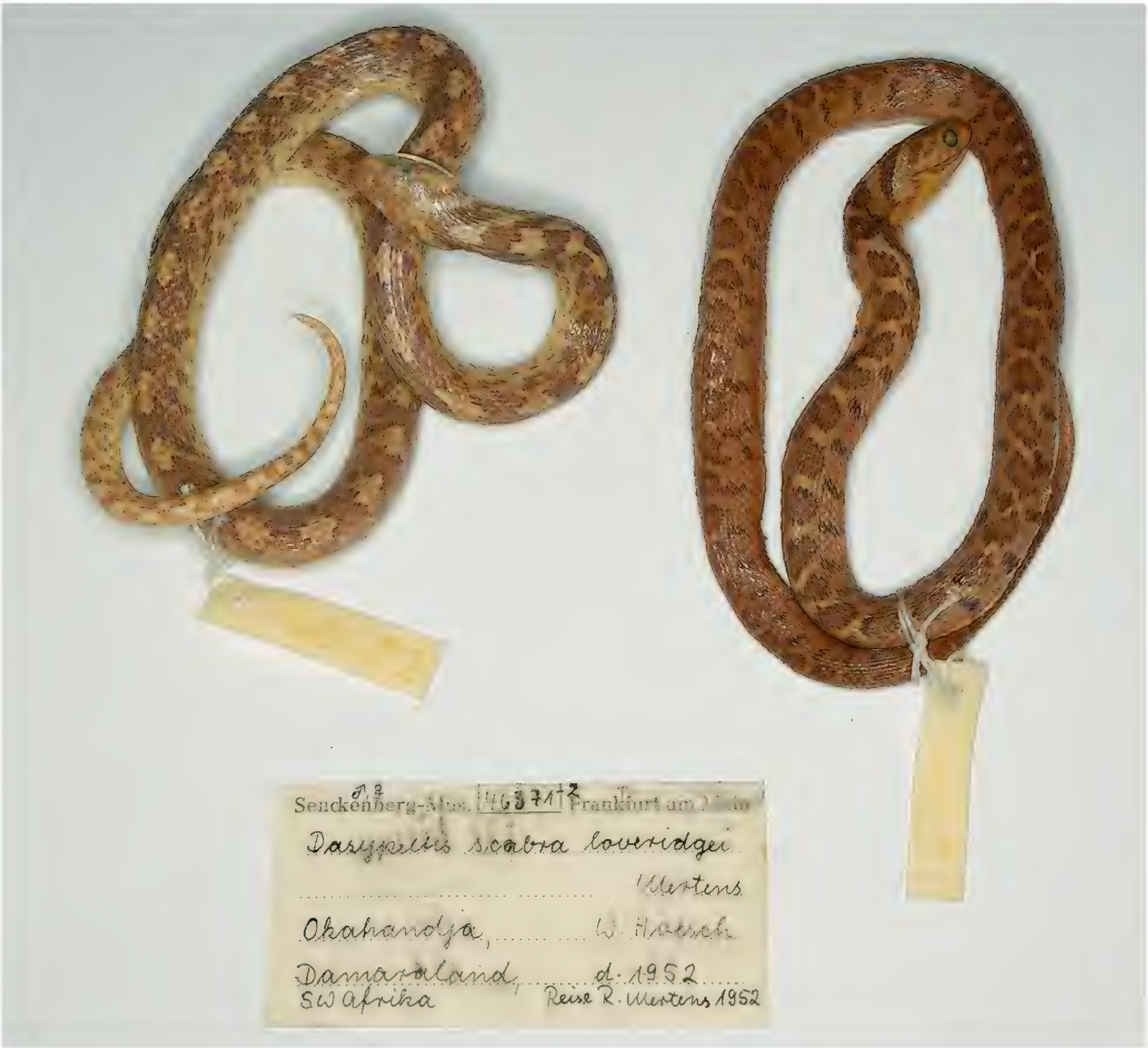

Fig. 13. Paratypes of *Dasypeltis loveridgei* Mertens, 1954 (SMF 46372 left, SMF 46371 right) from Okahandja, north of Windhoek, Namibia. SMF 46372 is a typical *D. loveridgei*, but SMF 46371 is a *D. scabra*. (Photo: Sebastian Lotzkat)

versus 467 + 98 = 565 mm (*D. scabra*). Elsewhere in its range, *D. scabra* may attain an even greater size (e.g., female from Kenya: 867 + 95 = 962 mm, see Bates & Broadley 2018). It therefore seems that *D. loveridgei* is indeed a slightly smaller species than *D. scabra*.

Regarding relative length of the tail, FitzSimons (1962) noted that it had been suggested that tail length of *D. loveridgei* was, on average, shorter than that of typical *D. scabra*. The present study indicated considerable overlap in values when comparing total length/tail length in males and females of each species (*D. loveridgei*: males 5.74–8.10, mean 6.89, females 7.33–10.26, mean 8.42; *D. scabra*: males 5.69–6.76, mean 6.25, females 6.93–9.12, mean 8.23), and this is therefore not a reliable character for distinguishing between them. There was also considerable overlap in ventral, subcaudal and midbody scale counts, so these are also not, independently, especially useful characters for separating the two morphotypes.

The present study also examined a few characters not previously considered useful for separating the two taxa in Namibia. Frontal shield: usually smooth to moderately pitted in *D. loveridgei* versus usually largely to extensively pitted in *D. scabra*; inter-prefrontal sulcus: shallow to moderate versus usually deep respectively; prefrontal: usually shorter than internasal versus usually longer; and rostral: top of scale usually only barely visible from above versus almost always distinct.

This analysis indicates that *D. scabra* occurs in the Woodland and Shrubland-Woodland Mosaic of north-eastern Namibia, extending into the higher-lying central parts of the country, with a single record in the south-west which may be associated with populations extending northwards from the Northern Cape Province of South Africa (see Bates et al. 2014; Broadley 1990). *Dasypeltis loveridgei* is widespread in the country but largely restricted to higher-lying areas mainly above 1000 m a.s.l. As noted above, the two species are sympatric at a few localities in central Namibia, and parapatric in several areas throughout the country. It should be noted that Goethel's (2015a,b) concept of *D. loveridgei* is somewhat confused. His map (Goethel 2015a) indicates that this species occurs only in south-western Namibia (i.e., excluding the type locality in the central part of the country) and a small part of the adjacent Northern Cape Province of South Africa, but he later (Göthel 2015b) states that it ranges northwards across Namibia to south-western Angola and may also occur in the South African provinces of Free State, Gauteng and North West.

The use of only one primary line of evidence (e.g., morphology) for distinguishing between species can be problematic especially when differences are small, and an integrative taxonomic approach using multiple lines of evidence is always preferable. However, the present study determined several largely consistent morphological differences between the two species. Therefore, using morphological characters (see Table 3) as operational criteria for species delimitation, together with the occurrence of the two morphs in sympatry in at least a few areas and allopatry in several areas (Fig. 5), with no obvious hybrids/intermediates, it is concluded that two species are present in Namibia, namely *D. scabra* and *D. loveridgei*. The correlation between dorsal pattern ('5N' for *D. scabra* and '6N' for *D. loveridgei*) and morphological characters is largely supported by the discriminant function analysis (Fig. 12, Tables 1–2).

Populations in southern Namibia and the Northern Cape Province of South Africa, as well as north-western Namibia and south-western Angola, with similarities to *D. loveridgei*, are currently being investigated as part of a study on the taxonomic status of *Dasypeltis* in the western half of southern Africa that involves both a molecular phylogeny and an analysis of morphological traits (Bates et al. in prep.).

Acknowledgements. I thank the late Donald Broadley for data on specimens of Namibian *Dasypeltis* examined by him; Cora Stobie for preparing the distribution map; Agnes Phindane for measuring specimens; and Aaron Bauer for access to old literature. The following museums and their curators and collection managers are thanked for providing access to specimens during my visits: California Academy of Sciences, San Francisco (Lauren Scheinberg and Erica Ely) in 2019; Ditsong National Museum of Natural History, Pretoria (Lauretta Mahlangu); Natural History Museum, London (Patrick Campbell) in 2011; Naturhistorisches Museum zu Wien, Vienna (Silke Schweiger) in 2017; Musée Royal de l'Afrique Centrale, Tervuren (Danny Meirte) in 2012; and Museum für Naturkunde, Berlin (Frank Tillack) in 2011. I also thank the following institutions for the loan of material: Ditsong National Museum of Natural History, Pretoria (Lauretta Mahlangu); Field Museum of Natural History, Chicago (Alan Resetar); National Museum of Namibia, Windhoek (Seth Eiseb and Mathilde Awases); Zoologisches Museum, Universität Hamburg, Hamburg (Alexander Haas); and Zoologische Staatssammlung München, Munich. Colour photographs of specimens were kindly provided by Senckenberg Naturmuseum, Frankfurt am Main (Sebastian Lotzkat, Joseph Vargas and Linda Mogk: type series of *Dasypeltis scabra loveridgei*), Field Museum of Natural History, Chicago (*D. scabra*: FMNH 64563, 64682, 65853-4; *D. loveridgei*: 57654, 64487), and Zoologisches Forschungsmuseum Alexander Koenig, Bonn (Morris Flecks: ZFMK 5426). A visit to the natural history museums in London and Berlin in September and October 2011 was funded by the Reptile Speciation Project (a South African National Research Foundation [NRF] grant to Krystal A. Tolley, South African National Biodiversity Institute, Cape Town), and a visit to the Royal Museum for Central Africa in Tervuren in October 2012 was made possible by an African Biodiversity Information Centre scholarship (special thanks to Danny Meirte).

REFERENCES

Alexander G, Marais J (2007) A Guide to the Reptiles of Southern Africa. Struik Publishers, Cape Town

Anon (2022) Namibias geography. Online at https://www.info-namibia.com/info/namibias-geography [last accessed 1 Aug. 2022]

Bates MF (2013) First records of the egg-eating snake *Dasypeltis confusa* Trape & Mané, 2006 in Nigeria and Chad, with range extensions for Ghana. Navorsinge van die Nasionale Museum, Bloemfontein 29 (2): 17–27

Bates MF, Broadley DG (2018) A revision of the egg-eating snakes of the genus *Dasypeltis* Wagler (Squamata: Colubridae: Colubrinae) in north-eastern Africa and south-western Arabia, with descriptions of three new species. Indago 34 (1): 1–95

Bates MF, Ineich I (2012) A new size record for the West African egg-eating snake *Dasypeltis gansi* Trape & Mane, 2006, with new distribution records. Navorsinge van die Nasionale Museum, Bloemfontein 28 (3): 41–48

Bates MF, Branch WR, Bauer AM, Burger M, Marais J, Alexander GJ, de Villiers MS (eds) (2014) Atlas and Red List of the Reptiles of South Africa, Lesotho and Swaziland. Suricata 1. South African National Biodiversity Institute, Pretoria

Bates MF, Broadley DG, Barlow A, Wüster W, Tolley KA (2009) Egg-eating snakes of the genus *Dasypeltis* in Southern Africa: how many species are there? Abstracts: 50th Aniversary Conference of the Zoological Society of Southern Africa, Illovo Beach, South Africa, 21–25 July 2009: 69–70

Branch B [WR] (1988) Field Guide to the Snakes and other Reptiles of Southern Africa. Struik Publishers, Cape Town

Branch B [WR] (1998) Field Guide to Snakes and other Reptiles of Southern Africa. Third edition. Struik Publishers, Cape Town

Broadley DG (1983) FitzSimons' Snakes of Southern Africa. Delta Books, Johannesburg

Broadley DG (1990) FitzSimons' Snakes of Southern Africa. Revised edition with addendum. Delta Books, Johannesburg

Clauss B, Clauss R (2002) Common Amphibians and Reptiles of Botswana: More than just creepy-crawlies. Gamsberg Macmillan Publishers, Windhoek

Table 3. Comparative morphological data for *Dasypeltis scabra* and *D. loveridgei* in Namibia. Asterisks indicate characters useful for distinguishing between the two species.

	Dasypeltis scabra		***Dasypeltis loveridgei***	
*dorsal pattern	'5N' in 91.8% *n* = 49		'6N' in 97.1% *n* = 104	
pattern cycles on back	41–66 51.7 ± 4.83 *n* = 47		36–65 47.3 ± 5.37 *n* = 99	
*dark markings on belly	2–3 rows on either side, or extensively marked, in 84.6% *n* = 26		0–1 rows on either side in 97.0% *n* = 66	
maximum size (snout-vent length + tail length)	♂ 467 SVL + 98 mm tail (TMP 39329) *n* = 15 ♀ 730 + 97 mm (NMWN 2292); 773 mm (NMWN 253) *n* = 21		♂ 445 + 75 mm (ZMB 5754) *n* = 38 ♀ 689 + 91 mm (JV 8646) *n* = 36	
*supralabials	7 [3,4] in 85.7% *n* = 49		6 [2,3] in 81.6% *n* =103	
*length of prefrontal compared to internasal	PF > IN in 90.5% *n* = 42		IN ≥ PF in 84.4% *n* = 90	
*rostral visible from above	Distinct in 97.6% *n* = 42		Barely visible in 93.1% *n* = 87	
*frontal texture	Largely to extensively pitted (States 3–4) in 76.6% *n* = 47		Smooth to moderately pitted (States 0–2) in 68.3% *n* = 101	
*sulcus between prefrontals	Deep in 68.1% *n* = 47		Shallow to moderate in 98.0% *n* = 102	
total length/tail length	♂ 5.69–6.76 6.25 ± 0.38 *n* = 14	♀ 6.93–9.12 8.23 ± 0.66 *n* = 19	♂ 5.74–8.10 6.89 ± 0.54 *n* = 38	♀ 7.33–10.26 8.42 ± 0.55 *n* = 35
ventrals	♂ 204–220 210.0 ± 4.36 *n* = 15	♀ 212–240 224.3 ± 6.72 *n* = 22	♂ 202–226 214.3 ± 5.38 *n* = 40	♀ 212–236 225.7 ± 6.25 *n* = 36
subcaudals	♂ 51–62 56.6 ± 3.32 *n* = 14	♀ 41–55 48.3 ± 3.61 *n* = 21	♂ 47–60 52.7 ± 3.00 *n* = 41	♀ 38–50 45.2 ± 2.80 *n* = 34
midbody scale rows	♂ 22–26 24.1 ± 1.28 *n* = 15	♀ 23–28 24.8 ± 1.15 *n* = 23	♂ 22–25 23.4 ± 0.78 *n* = 39	♀ 23–27 24.2 ± 0.97 *n* = 35

Danielson JJ, Gesch DB (2011) Global multi-resolution terrain elevation data 2010 (GMTED2010). US Geological Survey. Open-File Report, Vol. 2011–1073, pp. 1–26

De Quieroz K (1998) The General Lineage Concept of Species, Species Criteria, and the Process of Speciation. A Conceptual Unification and Terminological Recommendations. Pp. 55–75 in: Howard DJ & Berlocher SH (eds) Endless forms: species and speciation. Oxford University Press, USA

De Quieroz K (2007) Species Concepts and Species Delimitation. Systematic Biology 56 (6): 879–886

Dobiey M, Vogel G (2007) Venomous Snakes of Africa / Giftschlangen Afrikas. Terralog vol. 15. Edition Chimaira, Frankfurt am Main.

Elzen, van den P (1980) Die Schlangen Südwest-Afrikas in der Herpetologischen Abteilung des Zoologischen Forschungsinstitutes und Museums Alexander Koenig in Bonn. Bonner zoologische Beiträge 31 (3–4): 333–356

Escoriza D (2012) *Dasypeltis sahelensis* Trape & Mané, 2006. In: Martínez G, León R, Jiménez-Robles O, González De la Vega JP, Gabari V, Rebollo B, Sánchez-Tója A, Fernández-Cardenete JR, Gállego J (eds). Moroccoherps. Amphibians and Reptiles of Morocco and Western Sahara

FitzSimons VF (1962) Snakes of Southern Africa. Purnell & Sons, Cape Town

FitzSimons V[F] (1966) A check-list, with synoptic keys, to the snakes of southern Africa. Annals of the Transvaal Museum 25 (3): 35–79

FitzSimons VFM (1970) A Field Guide to the Snakes of Southern Africa. Collins, London

FitzSimons VFM (1974) A Field Guide to the Snakes of Southern Africa. Second edition. Collins, London

Frost DR, Hillis DM (1990) Species in concept and practice: Herpetological applications. Herpetologica 46 (1): 87–104

Gans C (1959) A taxonomic revision of the African snake genus *Dasypeltis* (Reptilia: Serpentes). Annales du Musée Royal du Congo Belge (Tervuren), (8vo, Sciences zoologiques) 74: 1–237

Gans C (1964) Further comments on the forms of the African snake genus *Dasypeltis* (Reptilia : Serpentes). Revue de Zoologie et de Botanique Africaines 69 (3–4): 279–295

Göthel H (2015a) Die Pazifisten unter den Schlangen – Afrikanische Eierschlangen der Gattung *Dasypeltis*. Draco 16 (61): 6–21

Göthel H (2015b) Die Eierschlangen-Arten Afrikas. Draco 16 (61): 78–92

IUCN Standards and Petitions Committee (2022) Guidelines for Using the IUCN Red List Categories and Criteria. Version 15. Prepared by the Standards and Petitions Committee. Online at https://www.iucnredlist.org/resources/redlistguidelines [last accessed 15 Jun. 2023]

Lampe E (1911) Erster Nachtrag zum Katalog der Reptilien- und Amphibien-Sammlung des Naturhistorischen Museums der Stadt Wiesbaden. Jahrbücher des Nassauischen vereins fur Naturkunde 64: 137–236

Marais J (1985) Snake Versus Man: A guide to dangerous and common harmless snakes of southern Africa. Macmillan South Africa, Johannesburg

Marais J (1992) A Complete Guide to the Snakes of Southern Africa. Southern Book Publishers, Halfway House

Marais J (2004) A Complete Guide to the Snakes of Southern Africa. Second edition. Struik Publishers, Cape Town

Marais J (2022) A Complete Guide to the Snakes of Southern Africa. Third edition. Struik Nature, Cape Town

Mendelsohn J, Jarvis A, Roberts C, Robertson T (2002) Atlas of Namibia: A portrait of the land and its people. David Philip Publishers, Cape Town

Mertens R (1954) Neue Schlangenrassen aus Südwes- und Südafrika. Zoologischer Anzeiger, Leipzig 152 (9/10): 213–219

Mertens R (1955) Die Amphibien und Reptilien Südwesafrikas. Aus den Ergebnissen einer im Jahre 1952 ausgeführten Reise. Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 490: 1–171

Peters W[CH] (1870) [dated 1869] Förtekning på de af J. Wahlberg i Damaralandet insamlade Reptilierna. Öfversigt af Kongliga Vetenskaps-Akademiens Forhandlingar 26 (7): 657–662

QGIS Development Team (2020) QGIS Geographic Information System. Open Source Geospatial Foundation Project. Online at http://www.qgis.org/ [last accessed 9 Sep. 2020]

Sabaj MH (2016) Standard symbolic codes for institutional resource collections in herpetology and ichthyology: an Online Reference. Version 6.5 (16 Aug. 2016). American Society of Ichthyologists and Herpetologists, Washington, D.C. Online at http://www.asih.org/ [last accessed 25 Oct. 2017]

Saleh M, Sarhan M (2016) The egg-eating snake (Colubridae: *Dasypeltis*) of Faiyum, Egypt, with the description of a new species. Bulletin de la Société Herpétologique de France 160: 25–48

Schleicher A (2015) Reptilien Namibias. Namibia Wissenschaftliche Gesellschaft/Kuiseb Verlag, Windhoek

Schleicher A (2018) Reptilien Namibias. Second edition. Namibia Wissenschaftliche Gesellschaft/Kuiseb Verlag, Windhoek

Schleicher A (2020) Reptiles of Namibia. Namibia Scientific Society/Kuiseb Publishers, Windhoek

Sternfeld R (1908) Mimicry bei afrikanischen Schlangen. Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin 1908: 89–91

Sternfeld R (1910a) Zur Schlangenfauna Deutsch-Südwestafrikas. Mitteilungen aus dem Zoologischen Museum in Berlin 5: 52–58

Sternfeld R (1910b) Mehrere Fälle von Mimikry bei afrikanischen Schlangen. Mitteilungen aus dem Zoologischen Museum in Berlin 5: 58–60

Sternfeld R (1910c) Die Fauna der deutschen Kolonien. Reihe IV: Deutsch-Südwestafrika. Heft 1. Die Schlangen Deutsch-Südwestafrikas. Zoologischen Museum in Berlin. Pp. I–IV, 1–45 + map

Trape J-F, Mané Y (2006) Le genre *Dasypeltis* Wagler (Serpentes: Colubridae) en Afrique de l'Ouest: description de trois espèces et d'une sous-espèce nouvelles. Bulletin de Société Herpetologique de France 119: 27–56

Trape S, Mediannikov O, Trape J-F (2012) When colour patterns reflect phylogeography: new species of *Dasypeltis* (Serpentes: Colubridae: Bogini) from West Africa. Comples Rendus Biologies 335: 488–501

Trape J-F, Mediannikov O, Chirio A, Chirio L (2021) Une nouvelle espèce de serpent mangeur d'oeufs du genre *Dasypeltis* Wagler (Squamata: Colubridae: Colubrinae) en Afrique centrale. Bulletin de Société Herpetologique de France 177: 65–80

Uetz P, Freed P, Aguilar R & Hošek J (eds) (2022) The Reptile Database. Online at http://www.reptile-database.org [last accessed 29 Jun. 2022]

Werner F (1902) Ueber westafrikanische Reptilien. Verhandlungen der kaiserlich-königleihen zoologisch-botanischen Gesellschaft in Wien 52: 332–348

APPENDIX I

(*electronic supplement, available at* www.zoologicalbulletin.de)

Appendix I. Size, scalation and colour pattern data for *Dasypeltis* from Namibia. Values in bold refer to characters examined/determined by the author. In some cases most or all data was obtained from Mertens (1954, ssuperscripted 1), Gans (superscripted 2) and D. G. Broadley (superscripted 3). In a few cases most characters were determined by the author, but some values were taken from Gans (1954, underlined) and Broadley (italicised). Values separated by a forward slash refer to left and right sides of the head, respectively. Abbreviations: Y = yes (i.e., deep), F = fair (i.e., moderate), N = no (i.e., shallow), SD = semi-divided, Und = undivided, Div = divided, fragm. = fragmented, IN = internasal, PF = prefrontal, + in column AA indicates extensive markings elsewhere on belly.

Bonn zoological Bulletin 72 (2): 185–199
2023 · Malik K. et al.
https://doi.org/10.20363/BZB-2023.72.2.185

ISSN 2190–7307
https://www.zoologicalbulletin.de

Research article

urn:lsid:zoobank.org:pub:B26AA2A1-089D-4CC3-89FE-6E2D61EFBA82

Key characteristics of selected *Drepanaphis* Del Guercio, 1909 (Hemiptera: Aphididae) species based on various identification methods

Kamila Malik [1], Gary L. Miller [2], Andrew S. Jensen [3] & Karina Wieczorek [4,*]

[1,4] *Institute of Biology, Biotechnology and Environmental Protection, Faculty of Natural Sciences, University of Silesia in Katowice, Bankowa 9, 40-007 Katowice, Poland.*
[2] *United States Department of Agriculture (USDA), Agricultural Research Service, Systematic Entomology Laboratory, Beltsville, Maryland, USA.*
[3] *Department of Entomology, California Academy of Sciences, San Francisco, California, USA.*
* *Corresponding author: Email: karina.wieczorek@us.edu.pl*

[1] urn:lsid:zoobank.org:author:A52691E1-AE82-4E86-8FB8-B85AD6DA5845
[2] urn:lsid:zoobank.org:author:84F6A612-BF2C-438D-845F-E1766058E850
[3] urn:lsid:zoobank.org:author:CA9AF6EA-C49F-4820-BDB0-83F4BDED3B12
[4] urn:lsid:zoobank.org:author:95A5CB92-EB7B-4132-A04E-6163503ED8C2

Abstract. The Nearctic genus *Drepanaphis* Del Guercio, 1909 currently includes 16 species with similar morphometric features, and three-dimensional structures may be important in species identification. The form (shape) of the dorsal abdominal tubercles, however, can be distorted by mounting on microscopic slides and this ultimately clouds diagnostic characters. This paper focuses on the identification of three species belonging to the genus *Drepanaphis*: *Drepanaphis acerifoliae* (Thomas, 1878), *D. kanzensis* Smith, 1941 and *D. sabrinae* Miller, 1937, to show the apparent differences of the structures of the examined individuals based on analysis of material deposited in museum collections and freshly collected material. To verify structural differences more precisely, we used Scanning Electron Microscopy to depict morphological characters accurately and DNA barcoding to analyze individuals at the molecular level.

Key words. COI, *Drepanaphis acerifoliae*, *Drepanaphis kanzensis*, *Drepanaphis sabrinae*, dorsal abdominal tubercle, SEM.

INTRODUCTION

The correct identification of species is a basis of systematic and biology because it is the starting point for most organismal research studies (Iverson 2022). When a specimen is collected in the field and becomes a museum specimen (or is included in any entomological collection), it should be properly prepared for its preservation. In addition, the appropriate conservation of collected specimens and their metadata provides an important source of information for wider taxonomic, biogeographic or molecular studies (Newbold 2010). However, morphological structures can become distorted by immersion in alcohol or after mounting on a microscope slide. Ultimately, this changes the morphology and can make species identification difficult. Comparison with type material is important because it not only confirms morphological species identifications but also provides temporal (e.g., date of collections), ecological (e.g., host plant), and geographical (e.g., collection locality) data. These data, especially locality, are fundamental for defining species as endemic / native, adventive/invasive, and sympatric/allopatric. They also aid in determining identity when compared to the known distribution of a species, or they can lead to hypothesizing a new species (Miller et al. 2018). For some species, however, it happens that the type material has been lost or is in poor condition, and the comparative analysis of morphometric features is impossible. In such cases, it is necessary to critically evaluate the species diagnostic characters and compare with as many similar museum specimens as possible, thereby clarifying its taxonomical status. When diagnostic characters are unclear or intraspecific phenotypic variation is large, the usability of DNA barcoding, i.e., sequencing a fragment of the mitochondrial cytochrome oxidase subunit I (COI) gene, has been used for additional diagnostic data in many animal groups for species identification (Hebert et al. 2003; Foottit et al. 2008; Kekkonen & Hebert 2014; Depa et al. 2012). Lastly, additional species diagnostic characters have been obtained from the comparison of micromorphological structures of closely related species using scanning electron microscopy (SEM) (Kumar et al. 2014). Thus, integrative taxonomy is a comprehensive framework to delimit and describe taxa by integrating information from different types of data and methodologies (Pante et al. 2015).

Received: 14.05.2023
Accepted: 07.11.2023

Corresponding editor: D. Ahrens
Published: 17.11.2023

Aphids (Hemiptera: Aphididae) are difficult to identify and taxonomically verify due to seasonal polymorphism and complicated life cycles. This is particularly the case for the largest aphid genera *Aphis* Linnaeus, 1758 and *Cinara* Curtis, 1835, where the similarities among species are so considerable, that species identification is often based on DNA sequence data (Jousselin et al. 2013; Chen et al. 2013, 2016).

Within the Aphididae, less speciose genera such as *Drepanaphis* Del Guercio, 1909 present challenges in morphological taxonomy. *Drepanaphis* is a Nearctic genus with 16 species (Favret 2023) having similar morphometric characters. A prominent feature of the dominant generation, the alate viviparous females, is the dorsal abdominal tubercles that are variably developed on abdominal tergites I–IV and often conspicuously pigmented. In addition to coloration of fore femora and wings, this feature is crucial in the determination of microscope slide-mounted specimens of *Drepanaphis* (Smith & Dillery 1968; Blackman & Eastop 2023). The dorsal abdominal tubercles are three-dimensional structures which often become distorted during microscope slide preparation. This complicates species identification using the available keys for species determination within *Drepanaphis*. Thus, species delimitation in this genus can be very challenging using only microscopic slide-mounted specimens deposited in entomological collections. In this study, based on the identification of selected species of *Drepanaphis*, we focus on: (1) describing and quantifying the differences in the appearance of the diagnostic structures by comparing microscopic slide-mounted specimens deposited in museum collections with fresh collected material and living specimens; (2) showing discrepancies in the dimensions of significant structures (e.g., size of dorsal abdominal tubercles); (3) presenting the detailed structure of the dorsal abdominal tubercles using SEM and; (4) use of mitochondrial COI for species verification at the molecular level.

MATERIALS AND METHODS

Data collection and taxon sampling

Fresh specimens of alate viviparous females of *Drepanaphis acerifoliae* (Thomas, 1878) (six individuals), *D. kanzensis* Smith, 1941 (six individuals) and *D. sabrinae* Miller, 1937 (six individuals) were preserved in 70% ethanol (Table 1). Species were initially identified based on diagnostic morphological features, including dorsal abdominal tubercles (Smith & Dillery 1968; Blackman & Eastop 2023), using a Nikon SMZ 25 stereoscopic microscope and photographed using a Nikon DS-Fi2 camera.

Additionally, we examined 61 mounted slides of alate viviparous females of the following species of the genus *Drepanaphis*: *D. acerifoliae* (45 slides), *D. kanzensis* (eight slides, including holotype from USNM) and *D. sabrinae* (eight slides) using a Nikon Ni-U light microscope and photographed with a Nikon DS-Fi2 camera.

Institutional abbreviations

CAS = Biologické Centrum AV ČR, v.v.i., České Budějovice, Czech Republic
MZLU = Lund University Biological Museum, Lund, Sweden
MNHN = Muséum national d'histoire naturelle, Paris, France
NHMUK = Natural History Museum, London, UK
USNM = U.S. National Museum of Natural History Aphidomorpha collection, located at the Henry A. Wallace Beltsville Agricultural Research Center, Beltsville, Maryland, USA
DZUS = Entomology collection of University of Silesia, Katowice, Poland
ZMPA = Zoological Institute, Polish Academy of Sciences, Warsaw, Poland

The detailed collection data are presented in Table 2.

Table 1. Collection records and GenBank accession numbers of the studied aphid species.

No	species	collection date /collector	host plant	locality	coordinates	collection	GenBank no.	reference
1	*Drepanaphis acerifoliae*	24.09.2022 Kamila Malik	*Acer rubrum*	Raleigh, North Carolina, USA	35.7822 -78.6365	DZUS 24/9.22_170	KR037245	(Gwiazdowski et al. 2015)
2	*Drepanaphis kanzensis*	21.09.2022 Kamila Malik	*A. saccharum*	Rahway, New Jersey, USA	40.6211 -74.2854	DZUS 21/9.22_171	OR573481	present study
3	*Drepanaphis sabrinae*	24.09.2022 Kamila Malik	*A. saccharum*	Raleigh, North Carolina, USA	35.7822 -78.6365	DZUS 24/9.22_172	OR575052	present study
4	*Dreapnosiphum aceris* (Walker)						KR029857	(Henry et al. 2015)

Table 2 (continued next two pages). List of analyzed species from museum collections.

No	species	country	state	locality	date collection	det.	leg.	host plant	collection
1	*Drepanaphis acerifoliae*	USA	Utah	Payson	18.06.1959	J.Holman	G.F.Knowlton	*Acer saccharinum*	CAS
2	*Drepanaphis acerifoliae*	USA	Utah	Payson	18.06.1959	J.Holman	G.F.Knowlton	*A. saccharinum*	CAS
3	*Drepanaphis acerifoliae*	USA	Utah	Payson	18.06.1959	J.Holman	G.F.Knowlton	*A. saccharinum*	CAS
4	*Drepanaphis acerifoliae*	USA	Utah	Payson	18.06.1959	J.Holman	G.F.Knowlton	*A. saccharinum*	CAS
5	*Drepanaphis acerifoliae*	USA	Utah	Payson	18.06.1959	J.Holman	G.F.Knowlton	*A. saccharinum*	CAS
6	*Drepanaphis acerifoliae*	USA	North Carolina	Raleigh	05.07.1959	C.F.Smith	C.F.Smith	*A. rubrum*	CAS
7	*Drepanaphis acerifoliae*	USA	North Carolina	Raleigh	06.07.1959	C.F.Smith	C.F.Smith	*A. rubrum*	CAS
8	*Drepanaphis acerifoliae*	USA	Minnesota	St.James	03.08.1960	Dillery&Smith		*A. saccharinum*	CAS
9	*Drepanaphis acerifoliae*	USA	Minnesota	St.James	03.08.1960	Dillery&Smith		*A. saccharinum*	CAS
10	*Drepanaphis acerifoliae*	USA	Utah	Provo	21.06.1960	Pintera	G.F.Knowlton	*Acer* sp.	CAS
11	*Drepanaphis acerifoliae*	USA	North Carolina	Franklin	26,06,1970	C.F.Smith		*A. saccharinum*	CAS
12	*Drepanaphis acerifoliae*	USA	Utah	Payson	18.06.1959	J.Holman	G.F.Knowlton	*A. saccharinum*	CAS
13	*Drepanaphis acerifoliae*	USA	Utah	Provo	21.06.1960	Pintera	G.F.Knowlton	*Acer* sp.	CAS
14	*Drepanaphis acerifoliae*	USA	Utah	Provo	21.06.1960	Pintera	G.F.Knowlton	*Acer* sp.	CAS
15	*Drepanaphis acerifoliae*	USA	Utah	Salt Lake City	21.06.1960	Pintera	G.F.Knowlton	*A. saccharinum*	CAS
16	*Drepanaphis acerifoliae*	USA	Utah	Salt Lake City	22.06.1960	Pintera	G.F.Knowlton	*A. saccharinum*	CAS
17	*Drepanaphis kanzensis*	USA	Maine	Presque Isle	10.09.1956	D.H.R.L	Simpson	*A. saccharum*	Biologické Centrum AV ČR
18	*Drepanaphis kanzensis*	USA	Kansas	Hiawatha	02.09.1960	Dillery&Smith	G.F.Knowlton	*A. saccharum*	CAS
19	*Drepanaphis acerifoliae*	USA	North Carolina	Raleigh	05.07.1959	C.F.Smith	C.F.Smith	*A. rubrum*	MZLU
20	*Drepanaphis acerifoliae*	Canada	Manitoba	Winnipeg	15.07.1974	A.G.Robinson		*A. saccharinum*	MZLU
21	*Drepanaphis acerifoliae*	Canada	Manitoba	Winnipeg	28.06.1961		A.G.Robinson	*A. negundo*	MZLU

Table 2 (continued).

No	species	country	state	locality	date collection	det.	leg.	host plant	collection
22	*Drepanaphis acerifoliae*	Canada	Quebec	Orsainville	20.08.1972	W.Quednau	W.Quednau		MZLU
23	*Drepanaphis acerifoliae*	USA	Florida	Gainesville	02.02.1961			*A. rubrum*	MZLU
24	*Drepanaphis acerifoliae*	USA	Maryland	Beltsville	29.06.1986	Danielsson-87	C.F.Smith	*A. saccharum*	MZLU
25	*Drepanaphis acerifoliae*	USA	Maryland	Beltsville	29.06.1986	Danielsson-87		*A. saccharinum*	MZLU
26	*Drepanaphis acerifoliae*	USA	Maryland	Beltsville	29.06.1986	Danielsson-87		*A. saccharinum*	MZLU
27	*Drepanaphis acerifoliae*		Maryland	Beltsville	29.06.1986	Danielsson-87		*A. saccharinum*	MZLU
28	*Drepanaphis acerifoliae*	USA	Maryland	Beltsville	29.06.1986	Danielsson-87		*A. saccharinum*	MZLU
29	*Drepanaphis acerifoliae*	USA	Maryland	Beltsville	29.06.1986	Danielsson-87		*A. saccharinum*	MZLU
30	*Drepanaphis acerifoliae*	USA	Maryland	Beltsville	29.06.1986	Danielsson-87		*A. saccharinum*	MZLU
31	*Drepanaphis acerifoliae*	USA	Maryland	Beltsville	29.06.1986	Danielsson-87		*A. saccharinum*	MZLU
32	*Drepanaphis acerifoliae*	USA	Maryland	Beltsville	29.06.1986	Danielsson-87		*A. saccharinum*	MZLU
33	*Drepanaphis acerifoliae*	USA	Maryland	Beltsville	29.06.1986	Danielsson-87		*A. saccharinum*	MZLU
34	*Drepanaphis acerifoliae*	USA	Maryland	Beltsville	29.06.1986	Danielsson-87		*A. saccharinum*	MZLU
35	*Drepanaphis acerifoliae*	USA	Maryland	Beltsville	29.06.1986	Danielsson-87		*A. saccharinum*	MZLU
36	*Drepanaphis acerifoliae*	USA	Maryland	Beltsville	29.06.1986	Danielsson-87		*A. saccharinum*	MZLU
37	*Drepanaphis kanzensis*	Canada	Quebec	Sainte-Foy	12.09.1970	W.Quednau	W.Quednau	*A. saccharum*	MZLU
38	*Drepanaphis acerifoliae*	USA	Maine	Orono	09.09.1976			*A. saccharinum*	MNHM
39	*Drepanaphis sabrinae*	USA	Maine	Orono	09.09.1976			*A. saccharum*	MNHM
40	*Drepanaphis acerifoliae*	USA	District of Columbia	North Carolina	22.10.1958			*A. rubrum*	USNM
41	*Drepanaphis kanzensis*	USA	Fort Scott	Kansas	17.06.1940		C.F. Smith	*A. saccharum*	USNM
42	*Drepanaphis sabrinae*	USA	North Carolina	Raleigh	10.11.1965			*A. saccharum*	USNM
43	*Drepanaphis acerifoliae*	USA	California	Lodi	04.02.1960	R.C.Dickson		*Acer* sp.	NHMUK

Table 2 (continued).

No	species	country	state	locality	date collection	det.	leg.	host plant	collection
44	*Drepanaphis acerifoliae*	USA	North Carolina	Cherokee	16.10.1961			*A. rubrum*	NHMUK
45	*Drepanaphis acerifoliae*	USA	North Carolina	Cherokee	17.10.1961			*A. rubrum*	NHMUK
46	*Drepanaphis acerifoliae*	USA	California	Berkeley	20.10.1963	D.H.R.L		*A. saccharinum*	NHMUK
47	*Drepanaphis acerifoliae*	USA	California	Berkeley	20.10.1963	D.H.R.L		*A. saccharinum*	NHMUK
48	*Drepanaphis kanzensis*	Canada	Ontario	Unionville	wrz.60	J.Sypkens		*A. rubrum*	NHMUK
49	*Drepanaphis kanzensis*	Canada	Ontario	Unionville	wrz.60	J.Sypkens		*A. rubrum*	NHMUK
50	*Drepanaphis kanzensis*	USA	Utah	Logan Canyon	03.10.1957			*A. grandidentatum*	NHMUK
51	*Drepanaphis sabrinae*	USA	North Carolina	Raleigh	05.07.1959	C.F.Smith		*A. saccharum*	NHMUK
52	*Drepanaphis sabrinae*	USA	North Carolina	Raleigh	05.07.1959	C.F.Smith		*A. saccharum*	NHMUK
53	*Drepanaphis sabrinae*	USA	North Carolina	Raleigh	05.07.1959	C.F.Smith		*A.saccharum*	NHMUK
54	*Drepanaphis sabrinae*	USA	North Carolina	Raleigh	05.07.1959	C.F.Smith		*A. saccharum*	NHMUK
55	*Drepanaphis sabrinae*	USA	North Carolina	Raleigh	05.07.1959	C.F.Smith		*A. saccharum*	NHMUK
56	*Drepanaphis sabrinae*	USA	Minnesota	Saint Paul	05.07.1959			*A. saccharum*	NHMUK
57	*Drepanaphis acerifoliae*	Canada	Ontario	London	22.06.1952	C.H.N.Smith		*A. saccharum*	ZMPA
58	*Drepanaphis acerifoliae*	USA	North Carolina	Raleigh	05.07.1959	C.F.Smith		*A. rubrum*	ZMPA
59	*Drepanaphis acerifoliae*	USA	North Carolina	Raleigh	05.07.1959	C.F.Smith		*A. rubrum*	ZMPA
60	*Drepanaphis acerifoliae*	USA	North Carolina	Raleigh	05.07.1959	C.F.Smith		*A. rubrum*	ZMPA
61	*Drepanaphis kanzensis*	Canada	Ontario	Ottawa	27.09.1952	C.H.N.Smith		*A. saccharum*	ZMPA

Measurements

The dorsal abdominal tubercles of 18 fresh individuals (six in *D. acerifoliae*, six in *D. kanzensis*, and six in *D. sabrinae*) were measured from the base of the tubercle to its tip in every pair of tubercles by a Nikon NIS Elements D 4.50.00 64-Bit software and presented in millimeters (mm). Measurement examples are illustrated in Fig. 9 G–I.

Due to the different condition of the slide mounted samples, dorsal abdominal tubercles of 36 individuals (16 in *D. acerifoliae*, eight in *D. kanzensis*, and 12 in *D. sabrinae*) were measured from the base of the tubercle to its tip in every pair of tubercles by a Nikon NIS Elements D 4.50.00 64-Bit software and presented in millimetres (mm).

Scanning electron microscopy

We prepared two individuals of *D. acerifoliae*, *D. kanzensis* and *D. sabrinae* for SEM analysis. Each specimen was stored in 70% ethanol prior to imaging. Dehydration was provided by ethanol series of 80%, 90%, 96% and two changes of absolute as follows: 20 minutes in 80% ethanol, 15 minutes in 90% ethanol, 10 minutes in 96% ethanol, and two baths in absolute ethanol 10 minutes. The dehydrated samples were dried, stuck on the tables, sprayed with 30 nm of gold, and imaged with the Phenom XL field emission scanning electron microscope (Phenom-World B.V., Eindhoven, The Netherlands).

DNA extraction, PCR amplification, sequencing and alignment

Sampled alate viviparous females (five individuals of *D. kanzensis* and *D. sabrinae*) were preserved in 96% ethanol and then used for genomic DNA extraction. All extraction procedure followed the A&A Biotechnology protocol provided by the manufacturer, using Sherlock AX extraction kit. The 5-prime end of the mitochondrial COI barcode region was amplified using the primers LCO1490 (Forward: 5'-GGT CAA CAA ATC ATA AAG ATA TTG G-3') and HCO2198 (Reverse: 5'-TAA ACT TCA GGG TGA CCA AAA AAT CA-3') (Folmer et al. 1994). The PCR reaction included Color OptiTaq PCR Master Mix (EURx) and was performed on a Biometra TProfessional Basic Gradient thermocycler. The thermal profile of the PCR reaction was: initial denaturation 94°C – 60 s; denaturation 95°C – 40 s, annealing 45°C – 45 s, elongation 72°C – 60 s, extension 72°C – 180 s, number of cycles: 35. The amplicons were sequenced in both directions at GenoMed Warsaw. Raw chromatograms were viewed using Chromas ver. 2.6.6 software (Technelysium Pty Ltd. 2004) and edited with MEGA11 (Tamura et al. 2021). Alignments were made for each gene using Clustal W (Larkin et al. 2007) using default settings. From obtained sequences, the best were selected for further analysis. The resulting sequences were deposited in the GenBank (Table 1).

RESULTS

(1) Differences in appearance of diagnostic structures by comparing microscopic slides deposited in museum collections with freshly collected material and living specimens.

Drepanaphis acerifoliae is characterized by long, finger-like dorsal abdominal tubercles (d.a.t.) I and III. *D. kanzensis* has large, black d.a.t. III, while *D. sabrinae* is distinguished by d.a.t. II and III being large and sub-equal. These are the most important morphological differences of the species used for identification (Smith & Dillery 1968; Blackman & Eastop 2023). However, initial verification of these species based on type specimens may not provide key information on diagnostic characteristics. For example, in the holotype of *D. kanzensis*, d.a.t. are invisible (Fig. 1A). Among the remaining analyzed material from museum collections d.a.t. III are distinct (Fig. 1B). Some, however, are deformed. For example, the tubercles may overlap, making the whole d.a.t asymmetrical (Fig. 1C), whereas d.a.t. II are short or weakly visible and d.a.t. I and IV are inconspicuous (Fig. 1C–E). *D. acerifoliae* with d.a.t. I–IV conspicuous and d.a.t. I, III long and finger-like (Fig. 2A), seems to be the most characteristic and easiest species to identify in the genus *Drepanaphis* (Smith & Dillery 1968). However, a comparative analysis of museum material shows that it is sometimes confused with *D. sabrinae* (Fig. 3A). In particular, d.a.t. of *D. acerifoliae* are sometimes deformed (Fig. 2B) or only one pair of four is visible (Fig. 2C). In the case of *D. sabrinae*, mostly all d.a.t. overlap (Fig. 3B–C) and it is difficult to determine which are largest or of equal length, as is noted in the key of Smith & Dillery (1968). Therefore, species determination may be difficult in the examination of traditional microscope slides for *Drepanaphis* species where three-dimensional structures in the form of dorsal processes are key features. A solution for more accurate species identification may be mounting the specimen in a lateral orientation. However, few examples of such preserved material have been found in museum collections (Fig. 4A–C).

The study of species based on the fresh, not slide-mounted material, allows for a more detailed analysis of the indicated structures. In specimens of *D. kanzensis* d.a.t. I–IV are all clearly visible (Fig. 5A–C), whereas d.a.t. II and IV were practically not visible on any specimens from museum collections studied. The comparison of the fresh materials of *D. acerifoliae* and *D. sabrinae* underscores the usefulness of the features of three-dimensional dorsal tubercles in distinguishing these species. In *D. acerifoliae*, all d.a.t. are visible, with clear proportion between each pair and reflecting the size included in the Smith & Dillery (1968) key: I and III the largest pair, II and IV smaller (Fig. 6A–C). In *D. sabrinae*, all d.a.t. are conspicuous, symmetric, and clearly proportional to each other (Fig. 7A–C). The arrangement of the dorsal tubercles is visible in every projection of the body and is best observed when the insect is in the lateral view (Figs 5A, 6A, 7A).

Live images further emphasize species differences. In the photographed individual of *D. acerifoliae* (Fig. 8A–C), color features such as red eyes, head and thorax reddish brown, light-colored abdomen and distinctly dark-bordered wing veins, are a unique combination of characters for this species. Morphological features, such as size and arrangement of dorsal tubercles, and wax markings are also visible. Macrophotography is, therefore, a good tool for identification and documenting the

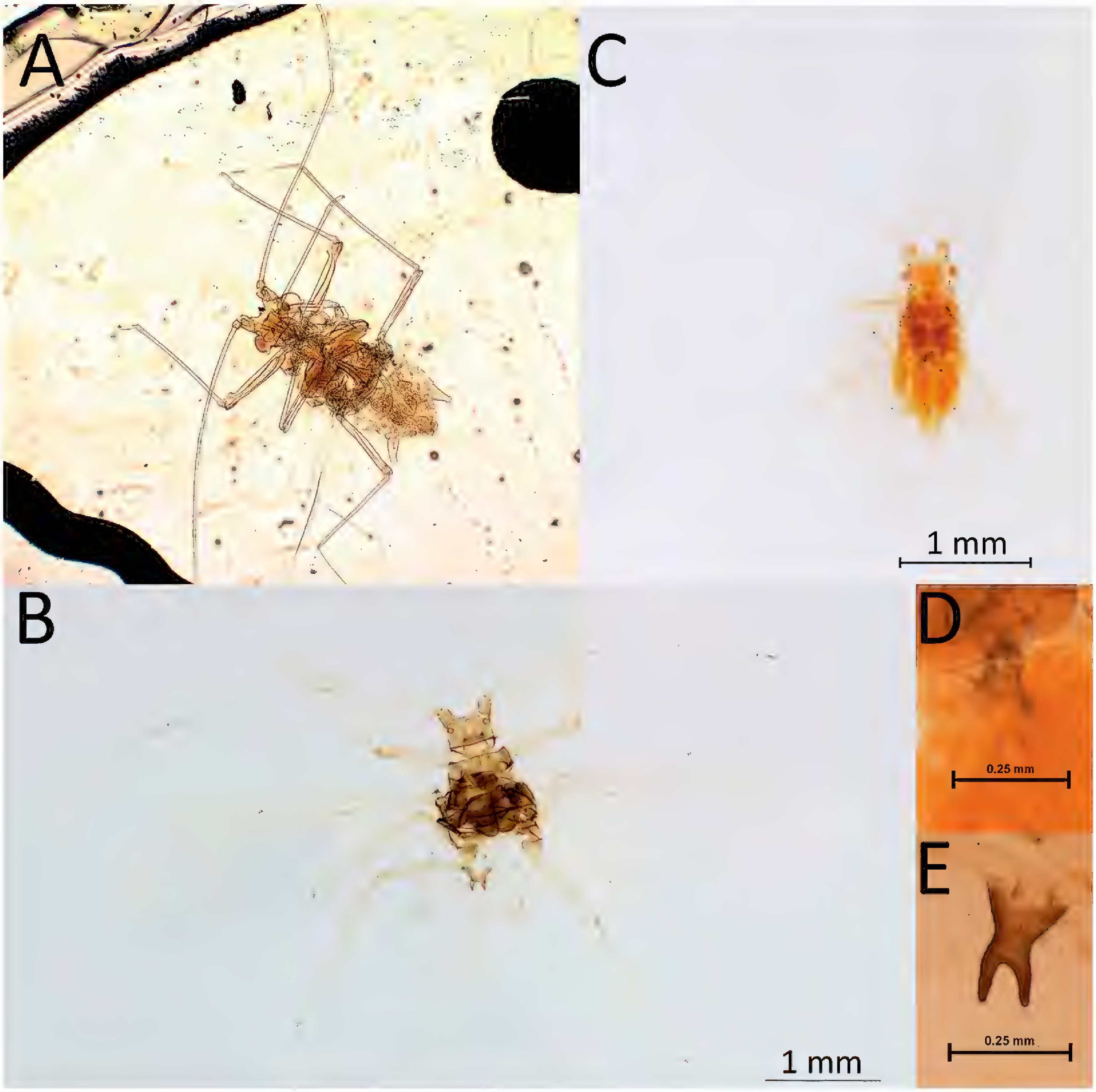

Fig 1. *Drepanaphis kanzensis* Smith, 1941. **A**. Holotype. **B**. Slide-mounted specimens with clearly visible dorsal abdominal tubercles. **C–E**. Slide-mounted specimens with deformed dorsal abdominal tubercles.

characteristics of species belonging to the genus *Drepanaphis*. It is, however, rarely used. Conversely, for some species such as *D. kanzensis* and *D. idahoensis*, which are entirely covered with white wax, this may not be a sufficient method to distinguish species (Fig. 8D–E).

(2) Discrepancies in the dimensions of key diagnostic structures – the size of dorsal abdominal tubercles

Smith and Dillery (1968) emphasized the importance of the size of the arrangement of d.a.t., as key features in the identification of aphids of the genus *Drepanaphis* (Fig. 9A–C). Often when analyzing individual museum specimens, it is difficult to measure the lengths of each d.a.t. because (I) the tubercles overlap and their placement is not visible, (II) the tubercles are not visible at all, (III) the tubercles are deformed by the microscope slide and it is difficult to determine size range (Fig. 9D–F).

In specimens of *D. kanzensis* from museum collections, only the third pair of tubercles is visible, while the second and third pairs are indiscernible (Fig. 9D). Measurements performed on fresh specimens in a lateral position make it possible to additionally measure the second and fourth pair of tubercles and in the case of this species they will be appropriate: II pair 0.07–0.11 mm, III pair 0.19–0.28 mm, IV pair 0.04–0.07 mm (Fig. 9G). In measurements carried out on eight individuals of this species from museum collections, it was possible to measure only the third pair of tubercles, the size of which was 0.2–0.28 mm (Table 3).

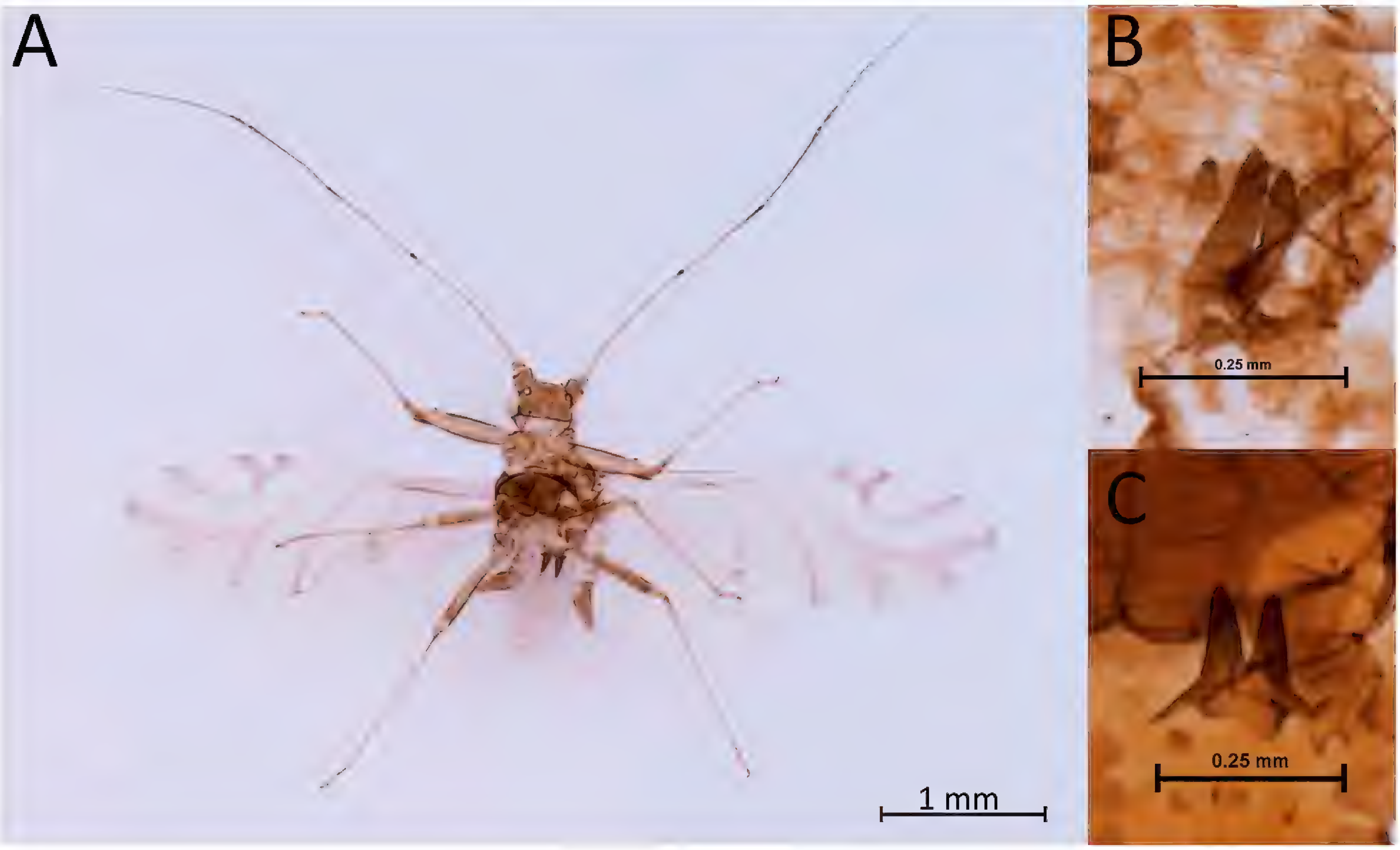

Fig 2. *Drepanaphis acerifoliae* (Thomas, 1878). **A**. Slide-mounted specimens with clearly visible dorsal abdominal tubercles (LM). **B–C**. Slide-mounted specimens with deformed dorsal abdominal tubercles (LM).

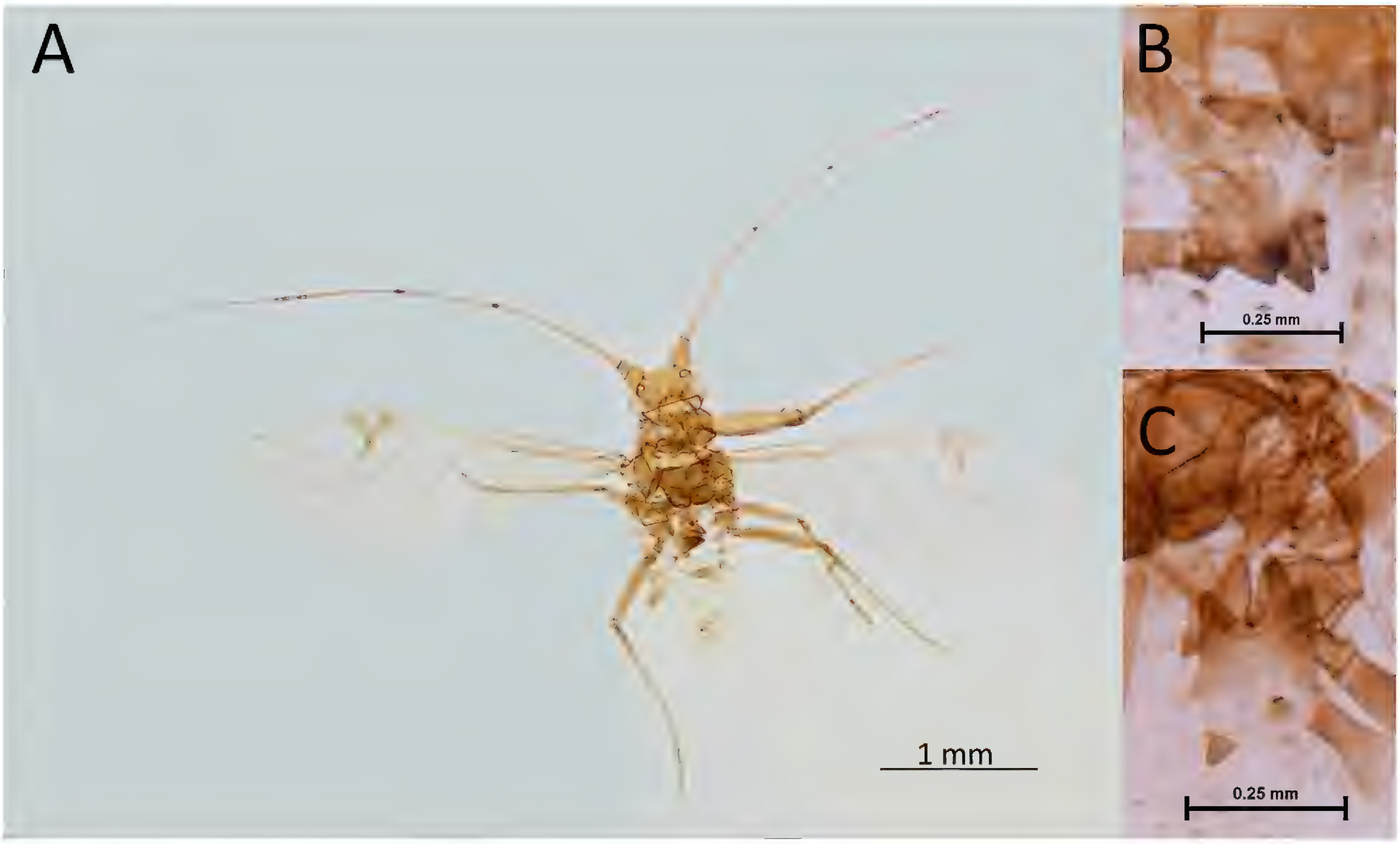

Fig 3. *Drepanaphis sabrinae* Miller, 1937. **A**. Slide-mounted specimens with clearly visible dorsal abdominal tubercles. **B–C**. Slide-mounted specimens with deformed dorsal abdominal tubercles.

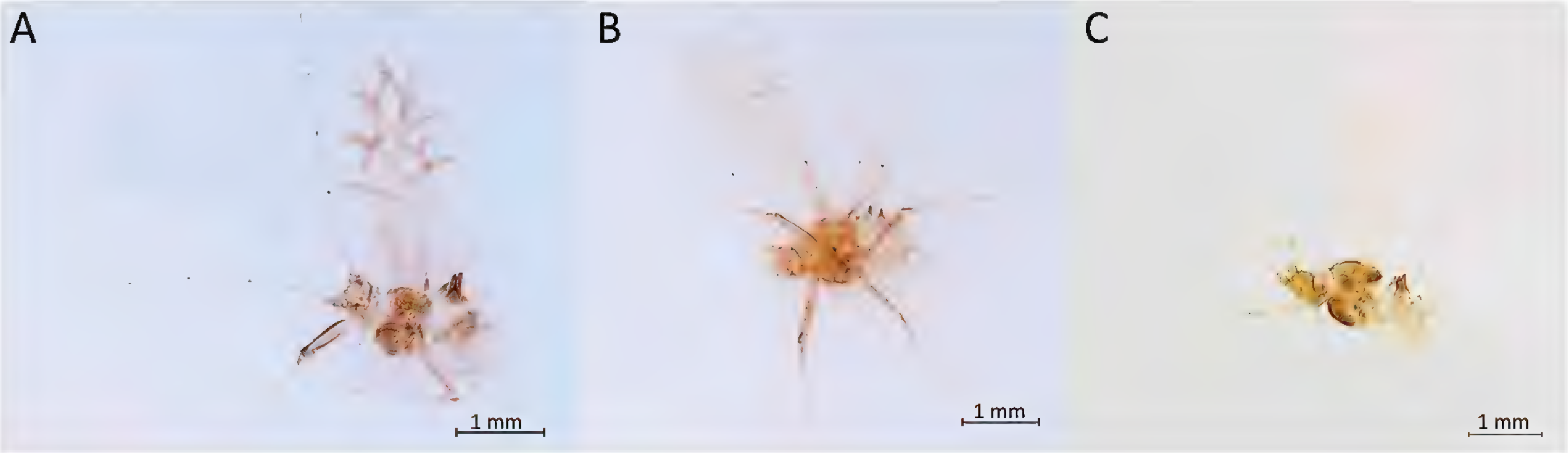

Fig 4. Lateral view of slide-mounted specimens. **A**. *Drepanaphis kanzensis* Smith, 1941. **B**. *Drepanaphis acerifoliae* (Thomas, 1878). **C**. *Drepanaphis sabrinae* Miller, 1937.

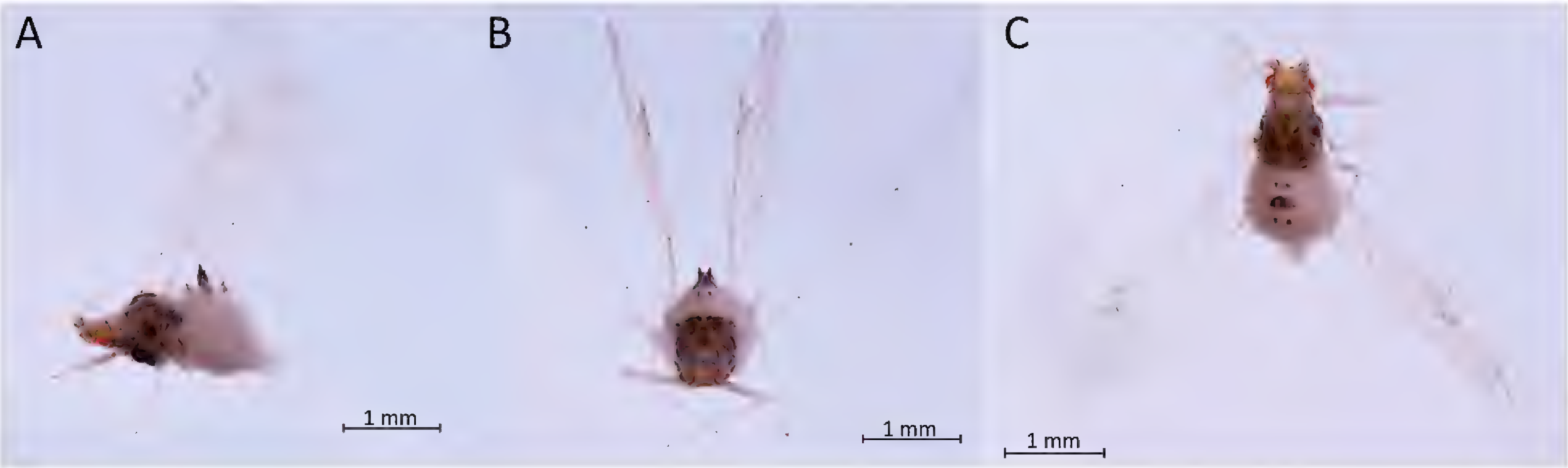

Fig 5. Fresh specimen of *Drepanaphis kanzensis* Smith, 1941. **A**. Lateral view. **B**. Frontal view. **C**. Dorsal view.

In the case of museum specimens of *D. acerifoliae*, it is difficult to measure the length of the second pair of tubercles for two reasons: (I) the tubercles of the second pair are lighter than the others, (II) the tubercles overlap. In half of the 16 specimens from museum collections measured we found it difficult to measure the second pair (Fig. 9E). When measuring fresh material, the second d.a.t. is clearly visible and an accurate measurement of 0.14 mm is possible (Fig. 9H). Good positioning of individuals on a microscope slide, including lateral position also gives similar results for tubercle measurements obtained from measurements of fresh material. Lengths of the tubercles of *D. acerifoliae* as follows: I pair 0.18–0.28 mm, II pair 0.07–0.14 mm, III pair 0.27–0.37 mm, IV pair 0.07– 0.15 mm (Table 3).

Measurements carried out on fresh *D. sabrinae* material make it possible, above all, to observe the proportions between selected tubercles. Because *D. sabrinae* is the only species in the genus *Drepanaphis* that has a second and third pair of equal length, it is necessary to carefully measure these structures. When measuring the material from museum collections, in four out of 12 individuals the second and third pairs of tubercles completely overlapped and they were impossible to measure (Fig. 9F).

Table 3. Measurements of the dorsal abdominal tubercles of *D. acerifoliae* (Thomas, 1878), *D. kanzensis* Smith, 1941 and *D. sabrinae* Miller, 1937 based on slide-mounted specimens and the fresh material.

No	species and number of individuals mounted/fresh	I pair of d.a.t		II pair of d.a.t		III pair of d.a.t		IV pair of d.a.t	
		mounted specimens	fresh specimens	mounted specimens	fresh specimens	mounted specimens	fresh specimens	mounted specimens	fresh specimens
1	*D. acerifoliae* n = 16/6	0.14–0.28	0.18–0.28	0.07–0.14	0.07–0.14	0.23–0.37	0.27–0.37	0.04–0.06	0.07–0.15
2	*D. kanzensis* n = 8/6	–	–	–	0.07–0.11	0.2–0.28	0.19–0.28	–	0.04–0.07
3	*D. sabrinae* n = 12/6	0.09–0.15	0.09–0.15	0.12–0.23	0.13–0.23	0.12–0.23	0.13–0.23	0.03–0.07	0.04–0.07

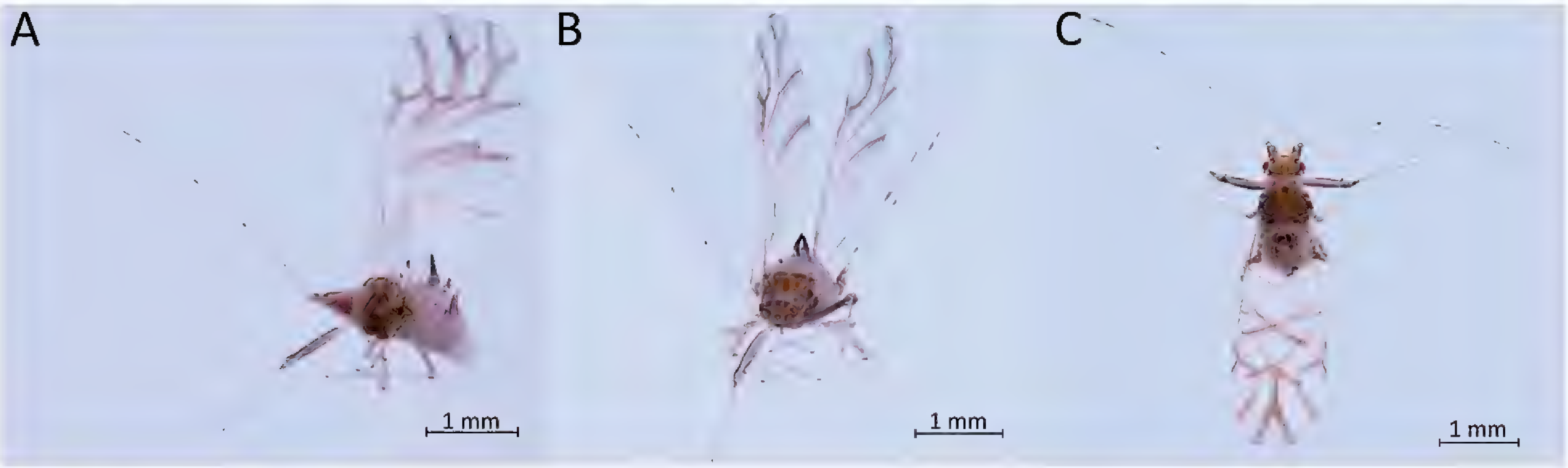

Fig 6. Fresh specimen of *Drepanaphis acerifoliae* (Thomas, 1878). **A**. Lateral view. **B**. Frontal view. **C**. Dorsal view.

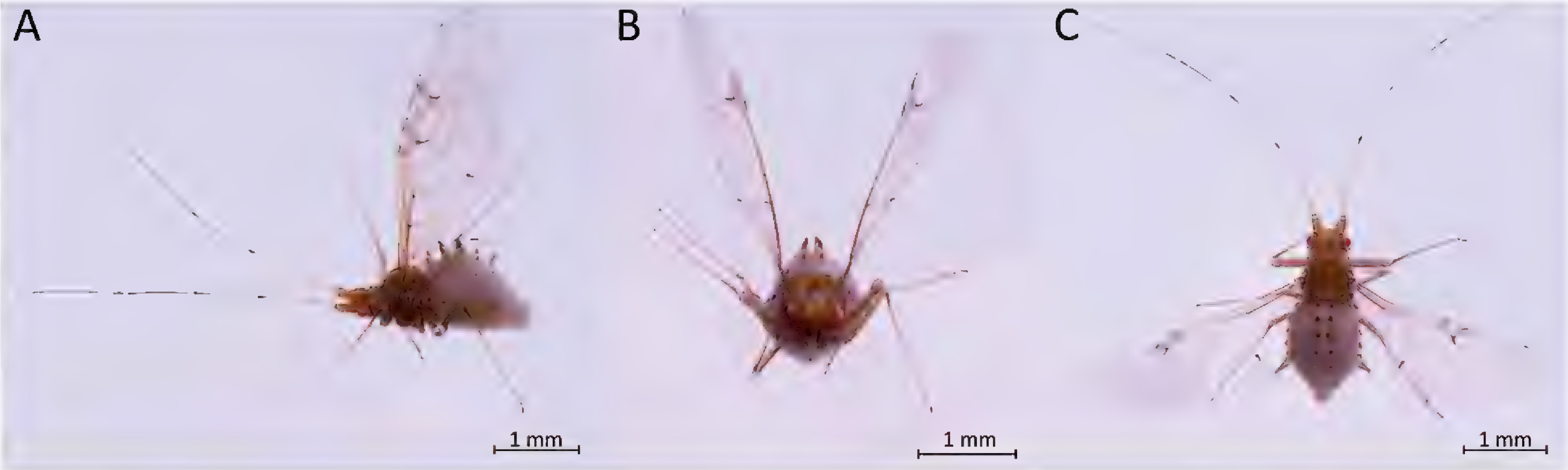

Fig 7. Fresh specimen of *Drepanaphis sabrinae* Miller, 1937. **A**. Lateral view. **B**. Frontal view. **C**. Dorsal view.

In the remaining individuals, the measurements were appropriate: I pair 0.09–0.15 mm, II pair 0.13–0.23 mm, III pair 0.13–0.23 mm, IV pair 0.04–0.07 mm (Fig. 9I). This also coincides with the dimensions of the tubercles obtained from measurements of fresh material of *D. sabrinae* (Table 3).

(3) Detailed structure of the dorsal abdominal tubercles using SEM

Verification of species using SEM techniques primarily allows for high magnification/resolution examination of the shape of the tubercles and their tips. On slide-mounted museum specimens only the general shape of the tubercles is visible. Even on the highest magnification, it is difficult to accurately identify the structures at their tips (Fig. 10A–C). Using SEM, we were able to measure the sensilla on the tips of tubercles in detail, whose size is 20–25µm. In addition, SEM images precisely illustrate the position of the tubercles on the abdomen, because the tubercles of each pair may grow on the abdomen independently or be connected at the base and branch at the tips. In *D. acerifoliae*, pairs of d.a.t. I, II and IV arise from the abdomen independently of each other. The third pair of d.a.t. is elongated and each of the tubercles branches less than half the length of the process (Fig. 10D). *D. kanzensis* also has a third pair of d.a.t. fused at the base and fork-branched at the ends (Fig. 10E). D.a.t. I and IV of *D. sabrinae* are independent and not fused basally; d.a.t. II and III are fused at the base (Fig. 10F).

(4) Mitochondrial COI as species verification at the molecular level

Our mitochondrial COI analysis further supported each of the three *Drepanaphis* species examined in this study as distinct species based on DNA sequence data. The interspecific pairwise genetic distances ranged from 7.14% to 10.55% (Table 4). These sequence divergences reflect the species differentiation sequence divergences of greater than 3% which are applicable for 96% of the Aphididae (Foottit et al. 2008).

DISCUSSION

Natural history collections are amazing resources that document the world's biodiversity in space and time (Miller et al. 2018). They are also an invaluable source for comparative research. *Drepanaphis* is an example of a genus characterized by few morphological features useful for species discrimination. Therefore, Smith and Dillery (1968) divided species described in this genus into five groups. The dorsal abdominal tubercles are a key diagnostic feature of the entire genus *Drepanaphis*. These structures are so unique that they are an import-

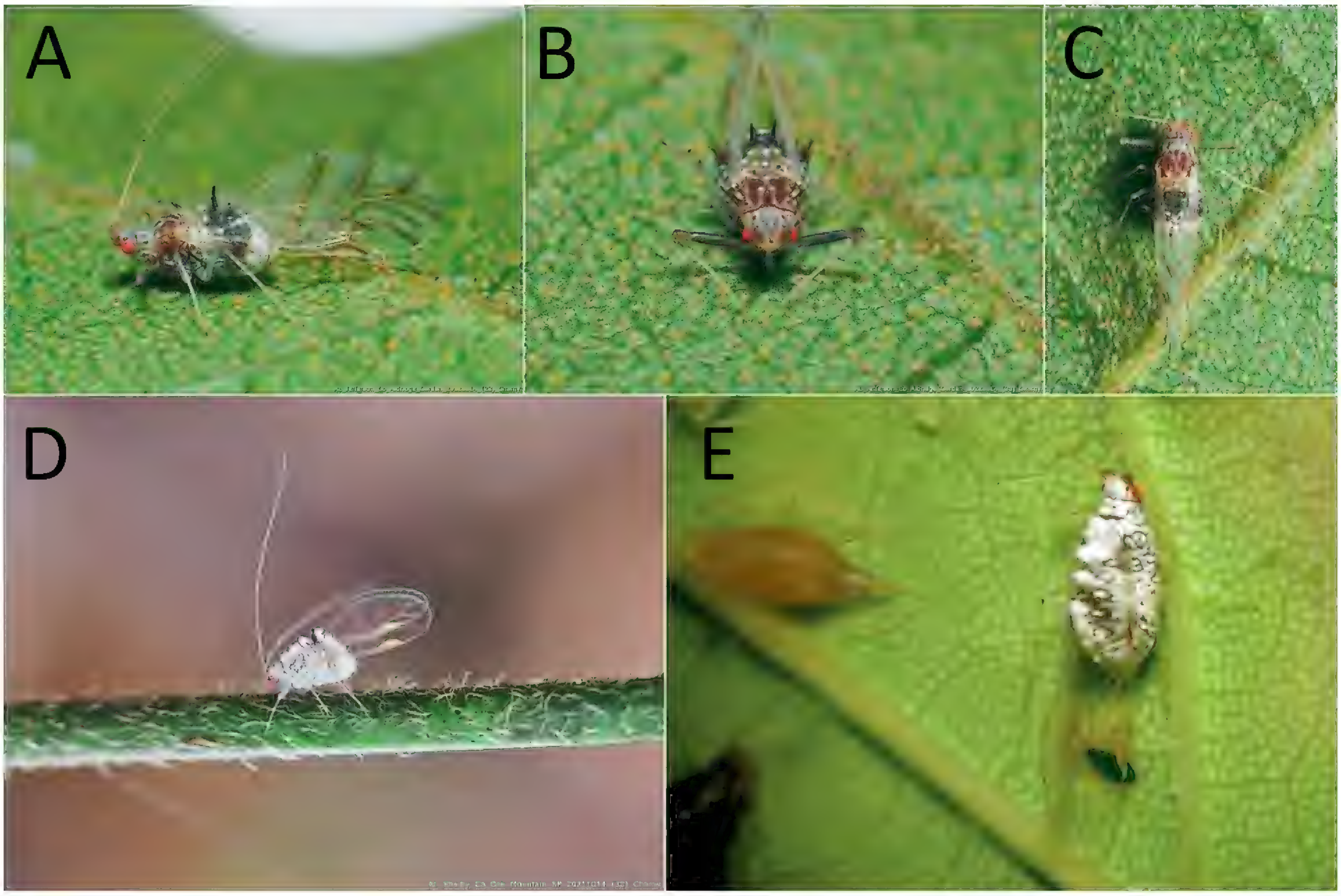

Fig 8. Live specimens. **A–C**. *Drepanaphis acerifoliae* (Thomas, 1878). **A**. Lateral view. **B**. Frontal view. **C**. Dorsal view. **D**. *Drepanaphis kanzensis* Smith, 1941, lateral view. **E**. *Drepanaphis idahoensis*, dorsal view. A–D. Image copyright V. Charny, under a Creative Commons 3.0 License.

ant starting point for identification. In this study, our data have shown that deformation of these structures can lead to misidentification of the species. In the sampled museum material from NHMUK, four slides (eight individuals) of *D. acerifoliae* were mistakenly labeled as *D. sabrinae*, and the latter confused with *D. carolinensis* Smith. *D. sabrinae* has pairs of tubercles II and III equal, whereas *D. acerifoliae* has the third pair largest. The latter arrangement occurred on these individuals which indicated wrong determinations. These three species were placed in a group named *acerifoliae*-group (Smith & Dillery 1968). Since host plants and morphometric features overlap in these species, the most important diagnostic feature is the size of the dorsal abdominal tubercles, which are usually distorted in microscope slides. In the case of species in which morphometric features fail, analysis of fresh material is required. Even though *D. kanzensis* has not been classified by Smith and Dillery (1968) to any of the species groups, some museum specimens (e.g., from NHMUK) were confused with *D. idahoensis*. In the field, *D. kanzensis* is all white (waxy) with clear wings, pale legs, and a large, black d.a.t. III. None of the other white species has clear wings with pale legs except *D. idahoensis*, which is western in its distribution in North America and has blunt rather than pointed d.a.t. setae (Smith & Dillery 1968). Correct identification of these two species, therefore, benefits from use of a combination of features resulting from macro- and microscopic observations. Preparation of lateral microscope slide mounts for *Drepanaphis* should also be used to avoid dorso-ventral distortion of abdominal tubercles. This would be espe-

Table 4. p-distance and nucleotide divergence (expressed as percentage) of studied species of the genus *Drepanaphis* Del Guercio, 1909.

	1	2	3
1 *Drepanaphis sabrinae*			
2 *Drepanaphis kanzensis*	7.14		
3 *Drepanaphis acerifoliae*	9.35	10.55	
4 *Drepanosiphum aceris*	15.69	13.83	13.28

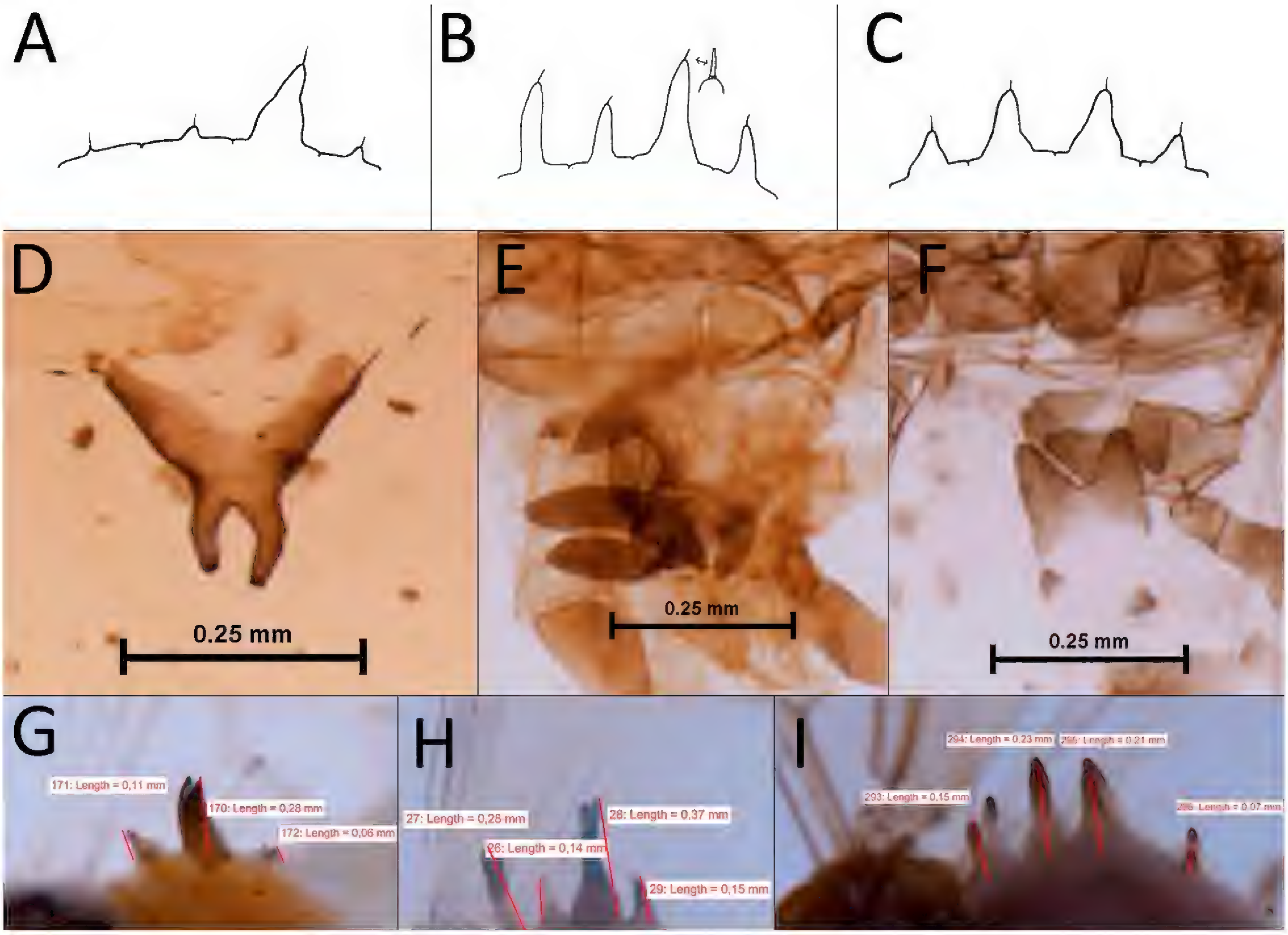

Fig 9. Dorsal abdominal tubercles. **A, D, G**. *Drepanaphis kanzensis* Smith, 1941. **B, E, H**. *Drepanaphis acerifoliae* (Thomas, 1878). **C, F, I**. *Drepanaphis sabrinae* Miller, 1937. **A–C**. Redrawn from the original description Smith & Dillery 1968. **D–F**. Slide-mounted specimens. **G–I**. Measured on the fresh specimens.

cially prudent for long series of specimens from a single sample.

Accurate morphometric measurements can also be useful in analyzing many groups of insects. Studies conducted by Seifert (2002) clearly indicate that careful measurements can distinguish even very similar species of ants. However, basic measuring errors occurring during stereomicroscope research may increase the percentage of individuals outside the range of interspecies overlap and correct identification (Seifert 2002). Comparisons of morphological characters, morphometric variables and morphometric ratios of type specimens and individuals from various localities were also successfully carried out for aphids. In particular, multivariate morphometric analyses (i.e., multiple discriminant analysis and the use of canonical variates) have demonstrated differences between closely related taxa or samples from clearly defined populations (Foottit et al. 2010; Wieczorek et al. 2017; Skvarla et al. 2020; Namgung et al. 2022). Due to the time-consuming process of taxonomic verification by morphological measurements, the interest in automatic identification of species has increased (Gaston & O'Neill 2004). For example, Yang et al. (2015) designed an identification system using insect wing outlines (DAIIS). The method provides a very high level of correct verification and a simple taxonomic tool especially for users who do not have extensive knowledge of algorithms and programing (Yang et al. 2015). However, the experiments were carried out only on individuals from the group Neuroptera and it is difficult to verify the effectiveness of the method on other winged insects. Automatic species verification is costly, which significantly limits its implementation in species classification (Gaston & O'Neill 2004). Such novel taxonomic approaches may not provide sufficient results on all groups, but it is promising in the case of insects represented only by the generation of winged viviparous fermales, as in the case of the genus *Drepanaphis*. Classical methods of species verification such a conventional light microscopy can be strengthened by detailed observations of body structures in SEM images. Evaluation of morphometric variation at the macro- and micro-morphological levels using SEM for taxonomic differentiation of closely related taxa of insects (including aphids) is increasingly used (Kanturski et al. 2015, 2018a, 2020, 2023; Mittné et al. 2022). Our SEM work with of *Drepanaphis* has resulted in morphological discernment and reveals new diagnostic features, such as the

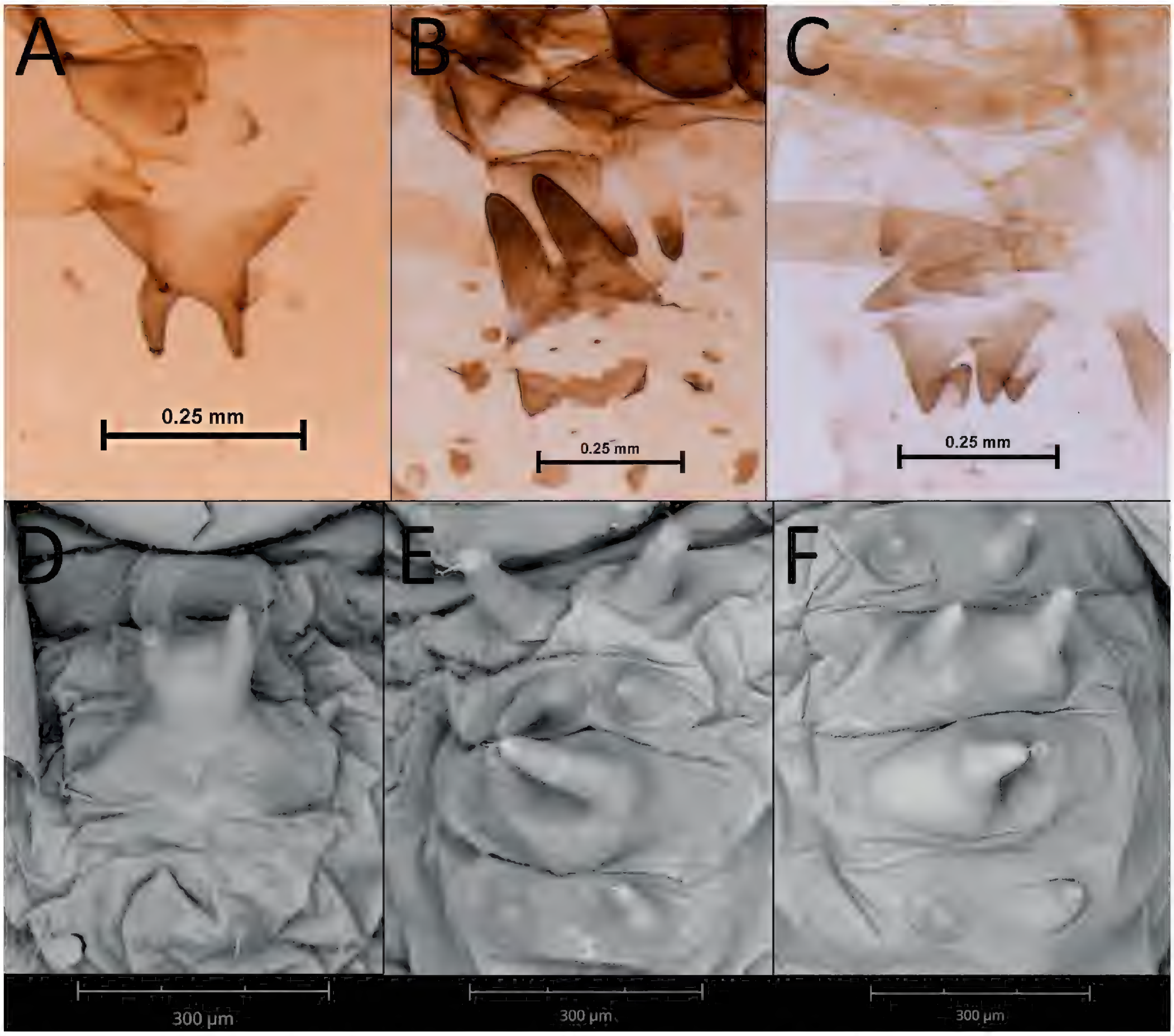

Fig 10. Dorsal abdominal tubercles. **A, D**. *Drepanaphis kanzensis* Smith, 1941. **B, E**. *Drepanaphis acerifoliae* (Thomas, 1878). **C, F**. *Drepanaphis sabrinae* Miller, 1937. **A–C**. Slide-mounted specimens in light microscopy. **D–F**. Specimens from scanning electron microscopy (SEM).

size of d.a.t sensilla and the position of each pair of the tubercles on abdomen.

The combination of precision morphological comparisons at the macro- and microscopic levels along with DNA sequence data add to our understanding of species delimitation. The most commonly used gene for species delimitation in animals is cytochrome c oxidase subunit I (COI) (Machida et al. 2017). COI species profile allows for 100% identification success even in one of the most taxonomically diverse groups of Lepidoptera, which show low sequence divergences (Hebert et al. 2003). Hebert et al. (2003) found that the distance between conspecific individuals of lepidopterans were always small, with an average intraspecific genetic distance of 0.25%. Later, the intraspecific genetic variation in other insect groups was mainly deduced from the DNA barcoding studies of various taxa (reviewed by Zhang & Bu 2022). In aphids, this effective tool was also widely used for species diagnosis, describing cryptic species or closely related species delimitation (Foottit et al. 2008; Lozier et al. 2008; Lee et al. 2017; Kanturski et al. 2018b; Théry et al. 2018; Barjadze et al. 2022; Massimino Cocuzza et al. 2022; Wieczorek & Sawka-Gądek 2023). On the other hand, genera morphologically similar or closely related and belonged to species groups known to present taxonomic difficulties (e.g., *Aphis*, *Brachycaudus*, *Dysaphis* or *Macrosiphum*) also characterize undifferentiated or overlapping barcodes, which limits of the standard COI barcode fragment for their identification (Coeur d'acier et al. 2014). COI has not been the only gene marker used for aphid DNA barcoding, other genes from the mitochondrial genome (e.g., COII, Cytb) and from endosymbionts have been used for various aphid groups (Lozier et al. 2008; Wang et al. 2011; Chen et al. 2012, 2013; Zhu et al. 2017).

Aphids are significantly economically important invasive pests throughout the world. Their correct identification is complicated by similarity among species, polymorphism, complex life cycles and host plant relationships. Relative 'size' of structures can also present some challenges that require statistical transformations for some measurements to be useful (Skavarla et al. 2020). Spectroscopic methods using the chemical composition of the body, heretofore little applied to aphids, may also be a means to achieve objective and quick identifications of an insect (Barbosa et al. 2018; Durak et al. 2022).

Species identification is essential for integrated management of pest aphids and for early detection and risk analysis of adventive species (Miller & Foottit 2017). Traditional morphological study can be inadequate with some aphid species determination. Therefore, integrated information from different sources like molecular data, morphological or biochemical characters, and ecological data can contribute substantially to effective identification of relatively homogeneous groups of species such as aphids of the genus *Drepanaphis*.

Acknowledgments. We are sincerely grateful to Paul A. Brown (NHM, UK), Daniele Matile-Ferrero, Adeline Soulier-Perkins, Thierry Bourgoin (MNHN, France), A. Bezděk (CAS, Czech Republic) and Jadranka Rota (MZLU, Sweden) for their kind help during the visits in the collections or for providing the opportunity to examine the material. We are very grateful to Vitaly Charny in USA for permitting us to use his image of live *Drepanaphis acerifoliae* and *D. kanzensis* available for use under creative commons licenses. Special thanks go to Joanna Zygała (UŚ, Katowice, Poland) for technical assistance in preparing SEM micrographs and to Christopher Owen (USDA, Systematic Entomology Laboratory) for his review and suggestions on the manuscript. Mention of trade names or commercial products in this publication is solely for providing specific information and does not imply recommendation or endorsement by the USDA. USDA is an equal opportunity provider and employer.

REFERENCES

Barbosa TM, de Lima LA, Dos Santos MCD, Vasconcelos SD, Gama RA, Lima KMG (2018) A novel use of infra-red spectroscopy (NIRS and ATR-FTIR) coupled with variable selection algorithms for the identification of insect species (Diptera: Sarcophagidae) of medico-legal relevance. Acta Tropica 185: 1–12. https://doi.org/10.1016/j.actatropica.2018.04.025

Blackman RL & Eastop VF (2023) Aphids of the world's plants: an online identification and information guide. Online at https://www.aphidsonworld-splants.info [last accessed 3 Mar. 2023]

Barjadze S, Halbert SE, Ben-Schlomo R (2022) A new gall-producing species of *Geoica* Hart, 1894 (Hemiptera: Aphididae: Eriosomatinae) from Israel. Zootaxa 5183 (1): 343–354. https://doi.org/https://doi.org/10.11646/zootaxa.5183.1

Chen R, Jiang LY, Qiao GX (2012) The effectiveness of three regions in mitochondrial genome for aphid DNA barcoding: a case in Lachininae. PLoS ONE 7 (10): e46190. https://doi.org/10.1371/journal.pone.0046190

Chen R, Jiang LY, Liu L, Liu Q, Wen J, Zhang RL, Li XY, Wang Y, Lei F, Qiao G (2013) The gnd gene of *Buchnera* as a new, effective DNA barcode for aphid identification. Systematic Entomology 38: 615–625. https://doi.org/10.1111/syen.12018

Chen R, Favret C, Jiang L, Quia GX (2016) An aphid lineage maintains a bark-feeding niche while switching to and diversifying on conifers. Cladistics 32 (5): 555–572. https://doi.org/10.1111/cla.12141

Coeur d'acier A, Cruaud A, Artige E, Genson G, Clamens A-L, Pierre E, et al. (2014) DNA Barcoding and the Associated PhylAphidB@se Website for the Identification of European Aphids (Insecta: Hemiptera: Aphididae). PLoS ONE 9 (6): e97620. https://doi.org/10.1371/journal.pone.0097620

Depa Ł, Mróz E, Szawaryn K (2012) Molecular identity of *Stomaphis quercus* (Hemiptera: Aphidoidea: Lachnidae) and description of a new species. European Journal of Entomology 109: 427–436. https://doi.org/10.14411/eje.2012.056

Durak R, Ciak B, Durak T (2022) Highly Efficient Use of Infrared Spectroscopy (ATR-FTIR) to Identify Aphid Species. Biology (Basel) 11(8): 1232. PMID: 36009859; PMCID: PMC9404783. https://doi.org/10.3390/biology11081232

Favret C (2023) Aphid species file. Online at http://aphid.speciesfile.org/HomePage/Aphid/HomePage.aspx [last accessed 10 Apr. 2023]

Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology 3 (5): 294–299.

Foottit RG, Maw HE, Von Dohlen CD, Hebert PDN (2008) Species identification of aphids (Insecta: Hemiptera: Aphididae) through DNA barcodes. Molecular Ecology Resources 8 (6): 1189–1201. https://doi.org/10.1111/j.1755-0998.2008.02297.x

Foottit RG, Maw HE, Pike KS, Miller RH (2010) The identity of *Pentalonia nigronervosa* Coquerel and *P. caladii* van der Goot (Hemiptera: Aphididae) based on molecular and morphometric analysis. Zootaxa 2358 (1): 25–38. https://doi.org/10.11646/zootaxa.2358.1.2

Gaston K & O'Neill M (2004) Automated species identification: Why not? Philosophical transactions of the Royal Society of London. Series B, Biological sciences 359: 655–67. https://doi.org/10.1098/rstb.2003.1442

Gwiazdowski R, Foottit R, Maw H, Hebert P (2015) The Hemiptera (Insecta) of Canada: Constructing a Reference Library of DNA Barcodes. PloS one. 10. e0125635. https://doi.org/10.1371/journal.pone.0125635

Hebert P, Cywinska A, Ball S.L, Dewaard J (2003) Biological identification through DNA barcodes. Proceedings of the Royal Society of London B 270: 313–321

Henry L, Maiden M, Ferrari J, Godfray Ch (2015) Insect life history and the evolution of bacterial mutualism. Ecology letters 18. https://doi.org/10.1111/ele.12425

Iverson J (2022) A review of Chelonian type specimens (order Testudines). Megataxa 7. https://doi.org/10.11646/megataxa.7.1.1

Jousselin E, Cruaud A, Genson G, Chevenet F, Foottit RG, Coeur d'Acier A (2013) Is ecological speciation a major trend in aphids? Insights from a molecular phylogeny of the conifer-feeding genus *Cinara*. Frontiers in zoology 10: 56. https://doi.org/10.1186/1742-9994-10-56

Kanturski M, Karcz J, Wieczorek K (2015) Morphology of the European species of the aphid genus *Eulachnus* (Hemiptera: Aphididae: Lachninae) – a SEM comparative and integrative study. Micron 76: 23–36. https://doi.org/10.1016/j.micron.2015.05.004

Kanturski M, Barjadze S, Jensen AS, Wieczorek K (2018a) A comparative morphological revision of the aphid genus *Myzaphis* van der Goot, 1913 (Insecta: Hemiptera: Aphididae) revealed a new genus and three new species. PLoS ONE 13 (3): e0193775. https://doi.org/10.1371/journal.pone.0193775

Kanturski M, Lee Y, Choi J, Lee S (2018b) DNA barcoding and a precise morphological comparison revealed a cryptic species in the *Nippolachnus piri* complex (Hemiptera: Aphididae: Lachninae). Scientific Reports 8, 8998. https://doi.org/10.1038/s41598-018-27218-2

Kanturski M, Świątek P, Trela J, Borowiak-Sobkowiak B, Wieczorek K (2020) Micromorphology of the model species pea aphid *Acyrthosiphon pisum* (Hemiptera, Aphididae) with special emphasis on the sensilla structure. The European Zoological Journal 87 (1): 336–356. https://doi.org/10.1080/24750263.2020.1779827

Kanturski M, Yeh HT, Lee Y (2023) Morphology, taxonomy, and systematic position of the enigmatic aphid genus *Sinolachnus* (Hemiptera: Aphididae, Lachninae). The European Zoological Journal 90 (1): 10–59. https://doi.org/10.1080/24750263.2022.2157897

Kekkonen M & Hebert PDN (2014) DNA barcode-based delineation of putative species: Efficient start for taxonomic workflows. Molecular Ecology Resources 14: 706–715. https://doi.org/10.1111/1755-0998.12233

Kumar V, Dakshina S, Osborn SL, McKenzie CL (2014) Coupling scanning electron microscopy with DNA bar coding: A novel approach for thrips identification. Applied Entomology and Zoology 49: 1–7. https://doi.org/10.1007/s13355-014-0262-2

Larkin MA, Blackshields G, Brown N, Chenna R, McGettigan PA, McWilliam H, Valentin F, Wallace IM, Wilm A, Lopez R, Thompson JD, Gibson TJ, Higgins DG (2007) Clustal W and Clustal X version 2.0. Bioinformatics 23: 2947–2948. https://doi.org/10.1093/bioinformatics/btm404

Lee Y, Lee W, Kanturski M, Foottit RG, Akimoto S-I, Lee S (2017) Cryptic diversity of the subfamily Calaphidinae (Hemiptera: Aphididae) revealed by comprehensive DNA barcoding. PLoS ONE 12(4): e0176582. https://doi.org/10.1371/journal.pone.0176582

Lozier JD, Foottit RG, Miller GL, Mills NJ, Roderick GK (2008) Molecular and morphological evaluation of the aphid genus *Hyalopterus* Koch (Insecta: Hemiptera: Aphididae), with a description of a new species. Zootaxa 1688 (1): 1–19. https://doi.org/10.11646/zootaxa.1688.1.1

Machida RJ, Leray M, Ho S.-L, Knowlton N (2017) Metazoan mitochondrial gene sequence reference datasets for taxonomic assignment of environmental samples. Scientific Data 4: 170027. https://doi.org/10.1038/sdata.2017.27

Massimino Cocuzza GE, Magoga G, Montagna M, Nieto Nafría JM, Barbagallo S (2022) European and Mediterranean Myzocallidini aphid species: DNA barcoding and remarks on ecology with taxonomic modifications in an integrated framework. Insects 13, 1006. https://doi.org/10.3390/ insects13111006

Miller G, Metz MA, Wheeler *Jr* AG (2018) What Is "There"? Searching for the North American Origin of the Aphid *Appendiseta robiniae*. American Entomologist 64 (4): 233–241. https://doi.org/10.1093/ae/tmy062

Miller GL, Foottit RG (2017) Pp. 627–639 in: The Taxonomy of Crop Pests: The Aphids. Foottit RG, Adler P (eds) Insect Biodiversity: Science and Society, Volume I, 2nd edition. Blackwell Publishingo. Zoologischer Anzeiger 302: 198–216. https://doi.org/10.1016/j.jcz.2022.11.012

Namgung H, Yu Y, Lee S, Kwon M, Kim J, Kim H (2022) Morphometric analysis of the wing for aphids (Hemiptera: Aphididae) associated with potatoes. Journal of Asia-Pacific biodiversity (online) 15 (2): 218–224. https://doi.org/10.1016/j.japb.2022.01.006

Newbold T (2010) Applications and limitations of museum data for conservation and ecology, with particular attention to species distribution models. Progress in Physical Geography 34: 3–22. https://doi.org/10.1177/0309133309355630

Pante E, Schoelinck C, Puillandre N (2015) From integrative taxonomy to species description: one step beyond. Systematic Biology 64 (1): 152–160. https://doi.org/10.1093/sysbio/syu083

Seifert B (2002) How to distinguish most similar insect species – improving the stereomicroscopic and mathematical evaluation of external characters by example of ants. Journal of Applied Entomology 126: 445– 454. https://doi.org/10.1046/j.1439-0418.2002.00693.x

Skvarla M, Kramer M, Owen CL, Miller GL (2020) Reexamination of *Rhopalosiphum* (Hemiptera: Aphididae) using linear discriminant analysis to determine the validity of synonymized species, with some new synonymies and distribution data. Biodiversity Data Journal 8:e49102. https://doi.org/10.3897/BDJ.8.e49102

Smith CF & Dillery DG (1968) The genus *Drepanaphis* Del Guercio (Homoptera: Aphididae). Annals of the Entomological Society of America 61: 185–204

Tamura K, Stecher G, Kumar S (2021) MEGA11: Molecular Evolutionary Genetics Analysis Version 11. Molecular biology and evolution. 38. https://doi.org/10.1093/molbev/msab120

Technelysium Pty Ltd. (2004) Technelsyim DNA Sequencing Software "Chromas". https://www.technelysium.com.au/chromas.html

Théry T, Kanturski M, Favret C (2018) Molecular data and species diagnosis in *Essigella* Del Guercio, 1909 (Sternorrhyncha, Aphididae, Lachninae). ZooKeys 765: 103–122. https://doi.org/10.3897/zookeys.765.24144

Wang JF, Jiang LY, Qiao G (2011) Use of a mitochondrial COI sequence to identify species of the subtribe Aphidina (Hemiptera, Aphididae). ZooKeys 122: 1–17. https://doi.org/10.3897/zookeys.122.1256

Wieczorek K, Bugaj-Nawrocka A, Kanturski M, Miller G (2017) Geographical variation in morphology of *Chaetosiphella stipae stipae* Hille Ris Lambers, 1947 (Hemiptera: Aphididae: Chaitophorinae). Scientific Reports (Nature Publishing Group) 7: 43988. https://doi.org/10.1038/srep43988

Wieczorek K, Sawka-Gądek N (2023) DNA Barcoding and Molecular Phylogenetics Revealed a New Cryptic Bamboo Aphid Species of the Genus *Takecallis* (Hemiptera: Aphididae). Applied Sciences 13: 7798. https://doi.org/10.3390/app13137798

Yang H, Ma CHS, Wen H, Zhan QB, Wang XL (2015) A tool for developing an automatic insect identification system based on wing outlines. Scientific Reports (Nature Publishing Group) 5: 12786. https://doi.org/10.1038/srep12786

Zhang H, Bu W (2022) Exploring large-scale patterns of genetic variation in the COI gene among Insecta: implications for DNA barcoding and threshold-based species delimitation studie. Insects 13(5): 425. https://doi.org/10.3390/insects13050425

Zhu XC, Chen J, Chen R, Jiang LY, Qiao GX (2017) DNA barcoding and species delimitation of Chaitophorinae (Hemiptera, Aphididae). ZooKeys 14 (656): 25–50. https://doi.org/0.3897/zookeys.656.11440

BHL

Blank Page Digitally Inserted

Bonn zoological Bulletin 72 (2): 201–208
2023 · Kirwan G.M. & Collar N.J.
https://doi.org/10.20363/BZB-2023.72.2.200

ISSN 2190–7307
https://www.zoologicalbulletin.de

Scientific note

urn:lsid:zoobank.org:pub:AFC76171-9BA7-478B-AEAB-0594A8806989

Lophornis melaniae Floericke, 1920 (Aves: Trochilidae), is a synonym of *L. stictolophus* Salvin & Elliot, 1873, not of *L. delattrei* (Lesson, 1839)

Guy M. Kirwan [1,*] & **Nigel J. Collar** [2]

[1,2] *Bird Group, Natural History Museum, Akeman Street, Tring, Herts. HP23 6AP, UK*
[2] *BirdLife International, Pembroke Street, Cambridge CB2 3QZ, UK*
[1] *Research Associate, Field Museum of Natural History, 1400 South Lakeshore Drive, Chicago, IL 60605, USA*
**Corresponding author: Email: GMKirwan@aol.com*

[1] urn:lsid:zoobank.org:author:D1A2DDD5-31B1-4F22-BE19-377A6E8B8A8E
[2] urn:lsid:zoobank.org:author:91CB1F94-B5DA-48B7-964E-FB336C20CAAF

Abstract. We re-evaluate the taxonomic status of a poorly known and largely ignored hummingbird taxon, *Lophornis melaniae* Floericke, 1920, which was described from two male syntypes. Reported to have been destroyed, these specimens survive in the Staatliches Museum für Naturkunde Stuttgart. None of the three commentators on this case inspected this material and only one read Floericke's original description. Comparison of the syntypes with specimen material and photographs available online of Rufous-crested Coquette *L. delattrei* (Lesson, 1839) and Spangled Coquette *L. stictolophus* Salvin & Elliot, 1873, suggests that, on the basis of its crest feathers being relatively densely packed and bushy rather than spiky, wiry and splayed, and on the broader distribution and greater number of dark spots on the crest, *L. melaniae* is a synonym of *L. stictolophus* rather than of *L. delattrei*, as had been postulated previously.

Key words. Trochilidae, *Lophornis*, *Lophornis melaniae*, hummingbirds, South America, Colombia.

In an illuminating commentary on the identity of an extremely little-known and largely ignored trochilid, *Lophornis melaniae* Floericke, 1920, Walters (1997) remarked that an accurate assessment of its taxonomic validity was impossible because the two male syntypes associated with this name "almost certainly no longer exist". On the authority of the mammalogist Dr Hans-Walter Mittmann, then employed by the Staatliches Museum für Naturkunde Karlsruhe, Walters (1997) reported that "Floericke's collection was stored at the Naturalienkabinett Stuttgart, and was completely destroyed during World War Two." However, this has proved to be incorrect: by speculatively interrogating the now defunct online database www.systax.org (originally at http://www.systax.org/de/details/tax/200311; now at GBIF: https://www.gbif.org/occurrence/1038115330 and https://www.gbif.org/occurrence/1038115306), in October 2021 GMK discovered that Floericke's types of *L. melaniae* are extant and held in the Staatliches Museum für Naturkunde Stuttgart (SMNS 30965 and SMNS 30966), where he examined and photographed them in May 2022 (Figs. 1–2).

Kurt (alternatively Curt) Floericke (1869–1934) studied natural sciences in Breslau and Marburg (1889–93) before commencing commercial trade in skins and live birds. He made a number of research and collecting trips, to the Balkans, Turkmenistan, Cyprus, Asia Minor, Morocco, Canary Islands and South America, some of them in the company of Otto Kleinschmidt (1870–1954), mainly in the period between 1898 and 1901 (Gebhardt 2006). To date, however, we have not found more specific details of these overseas expeditions, particularly to South America. From 1907 he was employed by the Stuttgart-based company Kosmos, and thereafter he was extraordinarily productive, writing several books and many hundreds of articles (not only on natural history topics) for popular magazines and specialist literature, including his Mitteilungen über die Vogelwelt [News about the Bird World], in which he published several descriptions of new taxa (Gebhardt 2006). SMNS holds 285 specimens from Floericke's collection (it is not clear if he took all of them himself or acquired them by other means), including the two *Lophornis melaniae* (F. Woog, Stuttgart, in litt., 2022). Additional material of his is also known to be held by museums in Bonn and Sarajevo, and was formerly also in Budapest prior to the 1956 fire (Roselaar 2003: 327).

The key passage in the original description of *Lophornis melaniae* reads as follows (translation from German by Isabelle Weiss and NJC, with our explanatory comments inserted in square brackets):

Received: 05.04.2023
Accepted: 13.11.2023

Corresponding editor: T. Töpfer
Published: 17.11.2023

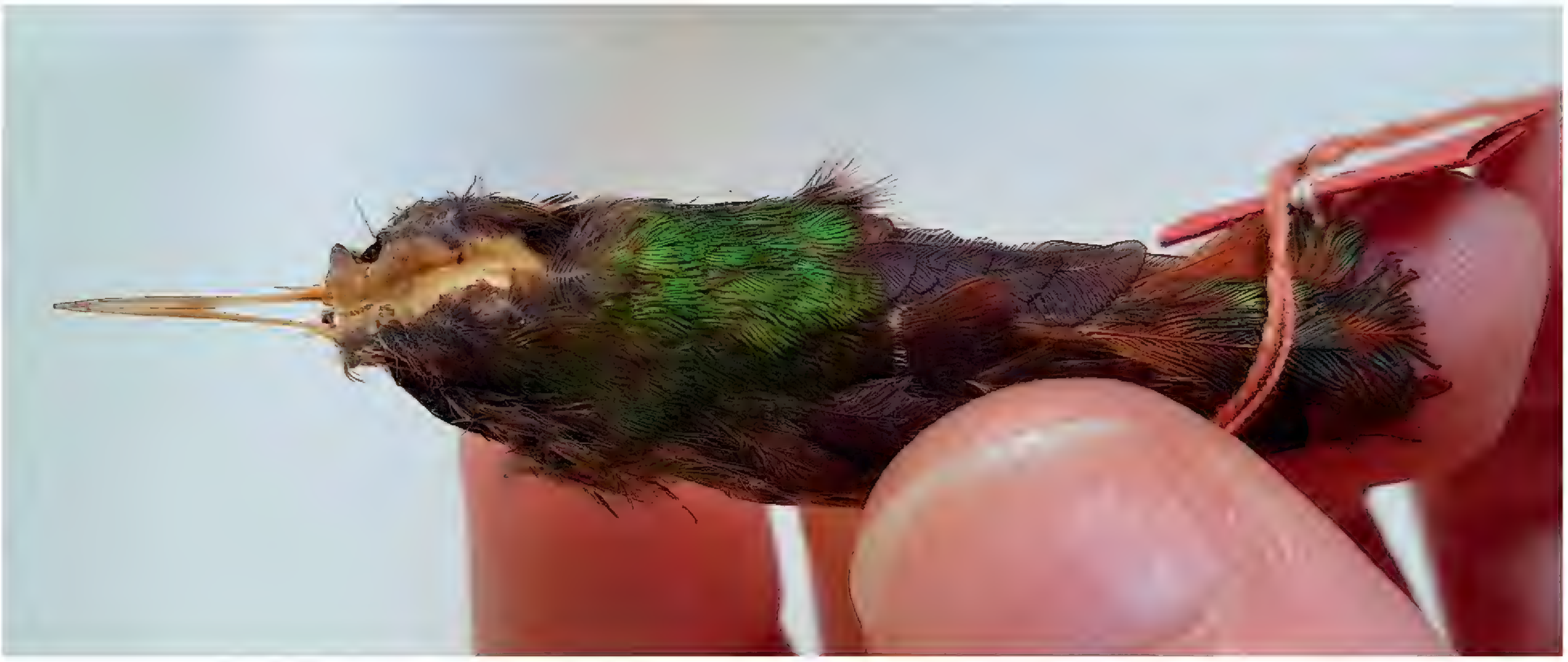

Fig. 1. Dorsal view of male syntype of *Lophornis melaniae*, SMNS 30965, held at the Staatliches Museum für Naturkunde Stuttgart (Guy M. Kirwan).

"…I have two male hummingbirds… which are more or less midway between *reginae* [*Lophornis reginae* Gould, 1847[1] = *L. stictolophus*] and *delattrei* as far as the formation of the 'cap' is concerned. Their crest feathers are narrow and pointed, but not nearly as ray-shaped or filiform as those of *delattrei*; they all or nearly all have the black terminal spot, but these are much smaller than in *reginae*, and they are about the size of a strong i-dot. Clearly one might think of these birds as hybrids between *reginae* and *delattrei* or as a colour aberration of one of them. However, this is contradicted by (1) the relatively frequent occurrence of this intermediate form, as I recall having had it in my hands several times before; (2) the colour of the crest feathers, which is not halfway between the two species but a shade paler than in *delattrei*, especially in the middle section, where it lightens to a pale isabelline-yellow; (3) the length of the bill, which is 9–9.5 mm in *reginae*, 9.5–10.5 mm in *delattrei*, but 11–12 mm in the intermediate form. Since all this argues for the latter's independence, I believe I must give it a new name and call it *Lophornis melaniae* in honour of my brave companion [his wife Melanie Reiß (1881–1971]. Types No. II, 2183 and 2184 of the collections of the Süddeutsche Vogelwarte [a private ornithological institute founded by Floericke]. I am not sure whether we are dealing here with three separate species or three local races (subspecies) of one and the same form. I tend to favour the latter view, and in this case all three forms would have to be called ternary. However, we cannot clarify this until we have precise information about the breeding ranges of the three forms. Nehrkorn's [1910] large catalogue, however, only lists eggs of *reginae* from Colombia."

From this description it is clear, as Floericke (1920) emphasises from the start, that the closest species morphologically to *L. melaniae* are the well-known species (Dickinson & Remsen 2013) Rufous-crested Coquette *L. delattrei* (disjunctly in Costa Rica and Panama; Central and East Andes of Colombia; and eastern Peru to northern Bolivia: Züchner 1999a) and Spangled Coquette *L. stictolophus* (northern Venezuela continuously south through eastern Colombia and Ecuador to northern Peru in the Marañón Valley: Züchner 1999b), but there has been no full review of either the specimen evidence

---

[1] *Trochilus reginae* von Schreibers, 1833, Collectanea ad Faunam Brasiliae, p. 1, Pl. 1, fig. 2, was thought to have potential priority over its synonym *Ornismya gouldii* Lesson, 1832, Les Trochilidées ou des Colibris et les Oiseaux-Mouches, p. 103, Pl. 36 = *Lophornis gouldii*, by Salvin & Elliot (1873), who thought both nomina dated from 1833 but nonetheless argued that the "established" name, *gouldii*, should take precedence. Their respective holotypes are in the Naturhistorisches Museum Wien (NMW 19.847, from Mato Grosso, Brazil: Schifter et al. 2007) and the Natural History Museum, Tring (NHMUK 1933.11.14.73, from Pará, Brazil: Warren 1966). In fact, whilst Lesson's plate dates from 1833, the name was first introduced in the text of the same work a year earlier, in 1832 (see Dickinson & Remsen 2013: 112, footnote 8). Because Schreibers' name is valid, to prevent homonymy in *Lophornis*, Salvin & Elliot (1873) introduced a new name, *stictolophus*, in place of *Lophornis reginae* Gould, 1847, Proceedings of the Zoological Society of London 1847: 95 – no type locality, although Gould (1861: lxiii) subsequently mentioned "New Granada" and a specimen from Zamora, in south-east Ecuador, but *stictolophus* was ascribed to "Columbia" (sic) by Salvin & Elliot (1873). Floericke (1920) evidently overlooked this or chose to ignore it. The holotype of Gould's name *reginae* appears to be lost. Authors of new hummingbird taxa were obviously scrabbling to invent new names during the era when large numbers of these remarkable birds started to reach Europe. Perhaps confusingly, Gould also named *Trochilus* (*Lophornis*) *regulus* Gould, 1846, Proceedings of the Zoological Society of London 1846: 89, but this name is a junior synonym of *Trochilus magnificus* Vieillot, 1817, Nouveau Dictionnaire d'Histoire Naturelle, Tome 7, p. 367; and *Lophornis regulus*, Gould, 1855, A monograph of the Trochilidae, Vol. 3, Pl. 120 and text, from Cochabamba, Bolivia, over which *Ornismya* (*Lophorinus*) *DeLattrei* Lesson, 1839, Revue Zoologique, par la Société Cuvierienne 2: 19, no type locality but probably from Peru, has priority (see Simon 1921: 285, Peters 1945: 32). Züchner (1999a) saw no rationale to treat Gould's name at subspecific rank, whereas Zimmer (1950) admitted this was a slight possibility.

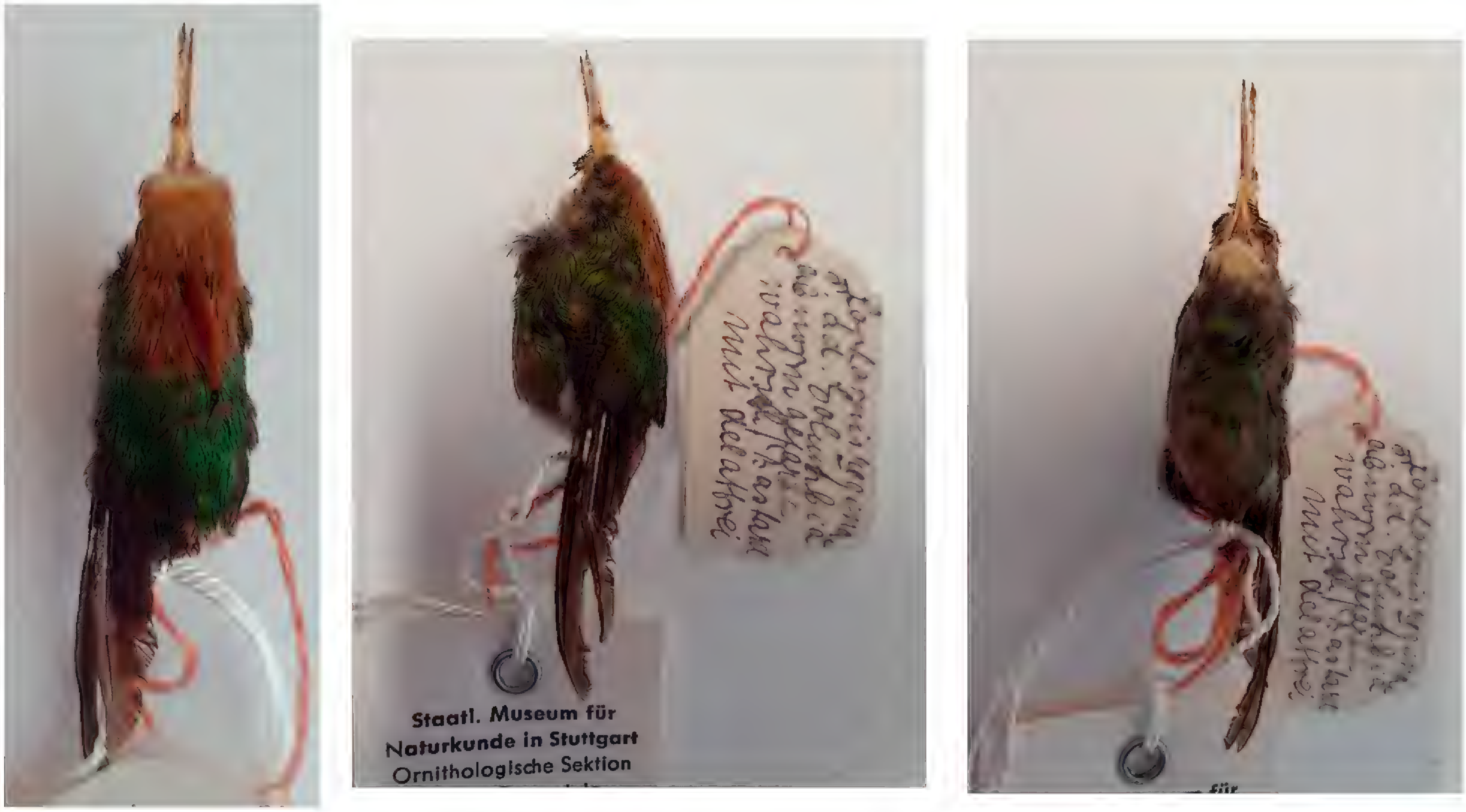

Fig. 2. Left to right, dorsal, lateral and ventral view of male syntype of *Lophornis melaniae*, SMNS 30966, held at the Staatliches Museum für Naturkunde Stuttgart (Guy M. Kirwan).

or the arguments that Floericke furnished to justify the position he chose to take.

Peters (1945) maintained *L. melaniae* as a species with a query, noting that he had not seen the original description but daring to speculate, without explanation, that *melaniae* might not even be a *Lophornis*. Unsurprisingly, he was unable to ascribe a range to the taxon, although the label of SMNS 30966 mentions "Colombia" (see below and Fig. 2). We have searched the catalogue of Floericke's bird collection published in parts in Mitteilungen über die Vogelwelt (starting in 1919 with volume 18), as this routinely included general localities (countries/states) for his specimens, but Floericke seems never to have completed this endeavour and there is no mention therein of these two individuals. Meyer de Schauensee (1966) treated *melaniae* as a species but found it "very doubtful", speculating that it represented a melanistic form of another species of *Lophornis*. However, as Walters (1997) noted, this was evidently based on an erroneous assumption: Floericke named the form for his wife, not because the specimens were melanistic, so Meyer de Schauensee's coining of the vernacular "Dusky Coquette" was entirely misplaced. Despite the inclusion of *L. melaniae* in these two seminal works, the only subsequent commentary on Floericke's taxon is that of Walters (1997) and it needs to be stressed that none of these authorities had seen the specimens in Stuttgart and evidently only Walters ever read the original description.

Walters (1997) speculated that *melaniae* must represent unusually pale-crested, faded or aberrant individuals of Rufous-crested Coquette *Lophornis delattrei* (also with reduced black spotting), citing (but not identifying by register number) a specimen of the latter species with these characters at the Natural History Museum, Tring (NHMUK). His conclusions were repeated by Züchner (1999a) and, consequently, by Dickinson & Remsen (2013) and del Hoyo & Collar (2014). Our own examination of specimens at Tring strongly suggests that the individual Walters had in mind was one of two skins stored apart from other *Lophornis* species and tentatively attributed to *melaniae*. They are now registered as NHMUK 2002.3.209 and NHMUK 2002.3.216, although both are Spangled Coquettes *L. stictolophus* from "Colombia" with pale, short crests (Fig. 3).

Males of *L. delattrei* and *L. stictolophus* are not always easily distinguished in the field, especially in brief views; however, the rufous crest of *L. stictolophus* is bushy rather than spiky (tips less pointed) and more prominently speckled with larger black or very dark green dots, which are scattered from the centre of the crown backwards (well captured in Schulenberg et al. 2007; Herzog et al. 2016). *Lophornis delattrei* has two subspecies: the nominate in Peru and Bolivia, and *L. d. lessoni* in Panama and Colombia. The latter reportedly differs in its more pointed crest feathers with almost no dark tips (Züchner 1999a). The depth of the colour of the crest varies in both species including both subspecies of *L. delattrei* (see Fig. 4 and photographs online, notably Macaulay Library [ML], https://macaulaylibrary.org/). However, while some accounts state that male *L. d. lessoni* has no or almost no

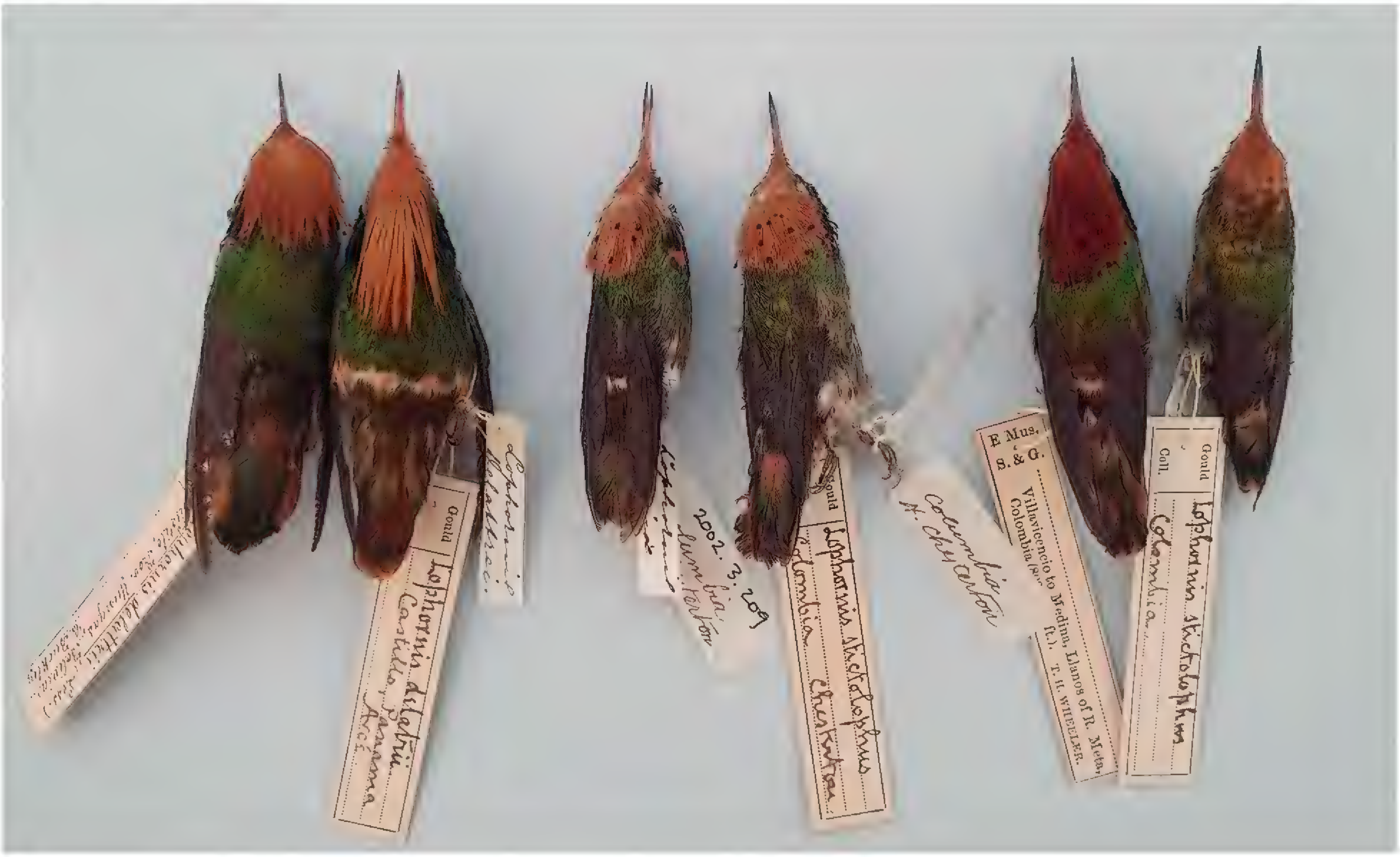

Fig. 3. Two male specimens of *Lophornis stictolophus* (middle pair), NHMUK 2002.3.209 and NHMUK 2002.3.216, considered to be similar to *L. melaniae* by Walters (1997), compared to typical males of *L. delattrei* (left-hand two, NHMUK 1887.3.22.1254 and NHMUK unregistered; note variation in crest feather length) and *L. stictolophus* (right-hand two, NHMUK 2002.3.225 and NHMUK 2002.3.212) (Guy M. Kirwan, © Trustees of the Natural History Museum, London).

dark spots in its crest (e.g., Hilty & Brown 1986; Züchner 1999a), a review of photos on ML suggests that c.10% of birds in Panama and Colombia possess visible spots (e.g., ML416172491, ML141020241). Conversely, an apparently much smaller percentage of individuals of the nominate subspecies have no (ML63329011) or almost no (ML205184961) visible spots (such that the validity of *lessoni* might be questioned: compare Figs. 4 and 5). A specimen of *lessoni* with many dark (green) tips to the crest feathers (Leibniz Institute for the Analysis of Biodiversity Change, Museum Koenig, Bonn, ZFMK Coll. Kl. 9845) came to Kleinschmidt via Graf von Berlepsch, and was originally in Floericke's hands, but it seems hard to consider the morphology of this individual as any way 'intermediate' (i.e., one of the specimens Floericke recalled handling in the past; see the original description). In both subspecies the dark is nearly always confined to the extreme tips (as specified and illustrated for the nominate by Schulenberg et al. 2007), but occasionally (e.g., ML284502131) with some additional small dark spots on the distal third of these feathers (based on specimens, field observations, and photographs of live birds on publicly accessible databases). Some illustrations (e.g., in del Hoyo et al. 1999) might suggest that there are differences in the tail pattern of males when viewed from below, but examination of specimens and photos, for example, ML506539681 (*delattrei*) and ML204920551 (*stictolophus*), does not support this.

The two syntypes of *Lophornis melaniae*, SMNS 30965 and SMNS 30966, are both males and more or less damaged, especially around their heads and bills, with 30965 now completely lacking feathers on the crown; they also lack multiple tail feathers, especially 30966 (Figs. 1–2). However, the bills are intact and measure respectively 13.3 and 13.5 mm, almost identical to the lengths of both *L. delattrei* and *L. stictolophus* (respective means of 10 and 12 males [including the two *melaniae*-like specimens] in NHMUK 12.5 and 13.2 mm: see Table 1), contra Floericke's own (and frankly baffling) finding quoted above from his original description. Given the damaged plumage of SMNS 30965, we have to trust Floericke's testimony, which clearly indicates that the two specimens were similar. Consequently, in the absence of a molecular analysis, the identity of *melaniae* must rest on the morphology of SMNS 30966, which is now labelled *stictolophus*. The crest feathers of this specimen are rather pale rufous but within the spectrum of variation shown by both species (e.g., ML204127541, *L. delattrei*; ML204103721, *L. stictolophus*). The dark spots are not profuse but some, especially in the centre of the crown, are rather large and bold, being twice the size of others (c.1.5 mm long; most are <1 mm), and a few are as close

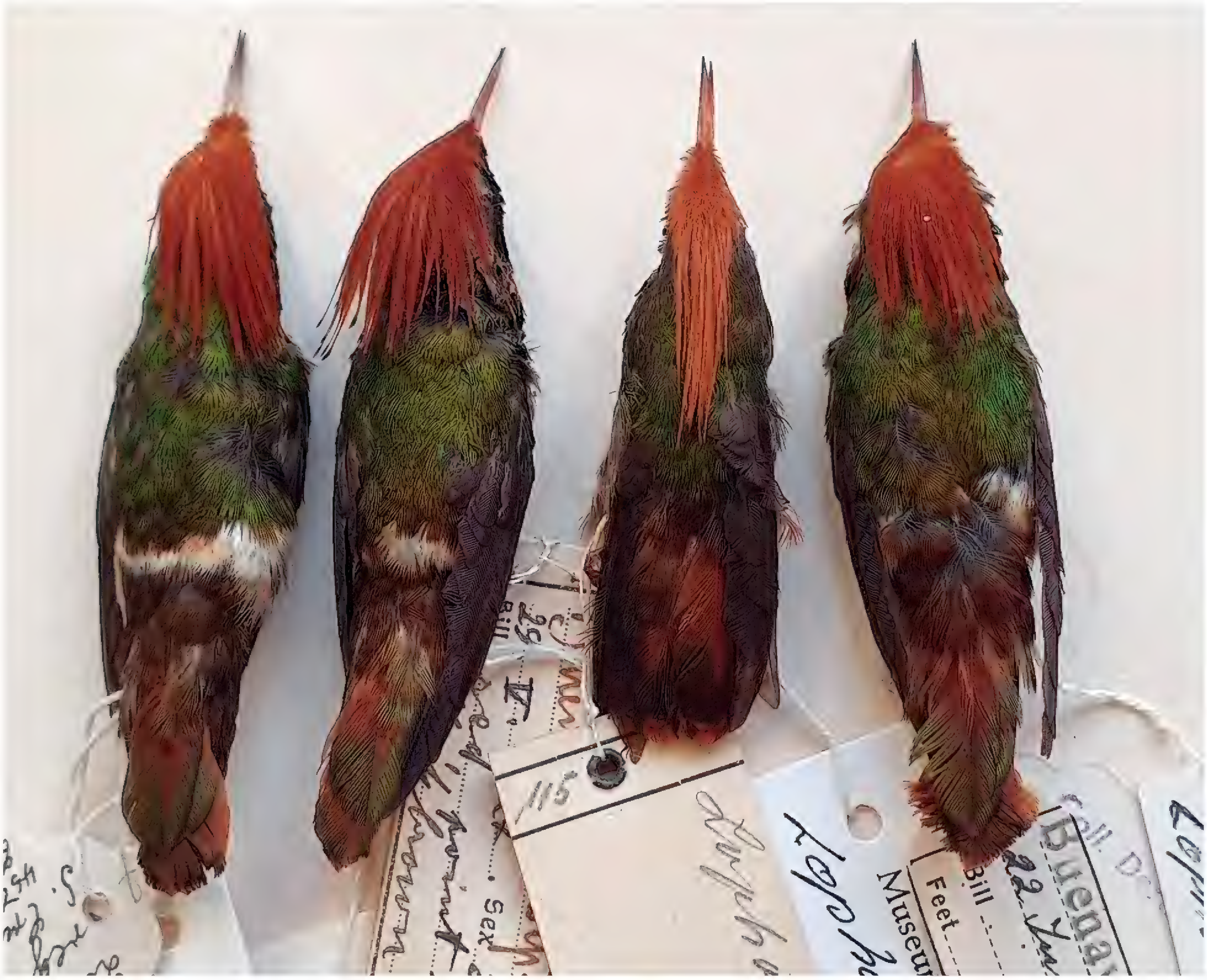

Fig. 4. Male specimens of *Lophornis d. delattrei* (Bolivia, at the Leibniz Institute for the Analysis of Biodiversity Change, Museum Koenig Bonn), from left to right ZFMK 10.080, ZFMK 10.076, ZFMK B^1.I.66.e.α and ZFMK 10.079 (Guy M. Kirwan).

to the base as to the tip of the relevant feather. Somewhat inconsistent with either *delattrei* or *stictolophus*, SMNS 30966 shows very few spots, even small ones, on the tips of the crest feathers, but two of them are adorned with comparatively large dark markings. We have not seen a specimen of either *delattrei* or *stictolophus* with an identical pattern of dark spots, but ML413454891 shows a *L. stictolophus* with relatively few dark-tipped feathers and perhaps equally sparse spotting across the rest of the crest, although none of the visible spots appears as large as in SMNS 30966. The crest feathers of SMNS 30966 form a rather densely packed mass (Fig. 2 left), without the typically wiry quality and splayed formation (even at rest, including in specimens) of *L. delattrei* (see, by contrast, Fig. 6).

Table 1. Bill length data (measured from tip of culmen to skull; i.e., measurement ‘Bsk’ per Eck et al. 2011) from specimens of *Lophornis stictolophus* and *L. delattrei* (subspecies combined) held in the Natural History Museum, Tring, compared with data for the syntypes of *L. melaniae* held at the Staatliches Museum für Naturkunde Stuttgart, all taken by GMK. Data (in mm) are presented in the format: mean with standard deviation (range, number of specimens). The specimens of *L. stictolophus* include the two individuals thought by Michael Walters to be similar to Floericke’s types.

Lophornis stictolophus	***Lophornis delattrei***	***Lophornis melaniae* SMNS 30965**	***Lophornis melaniae* SMNS 30966**
13.22 ± 0.74 (12.3–14.5, n = 12)	12.53 ± 0.96 (11.7–14.8, n = 10)	13.3	13.5

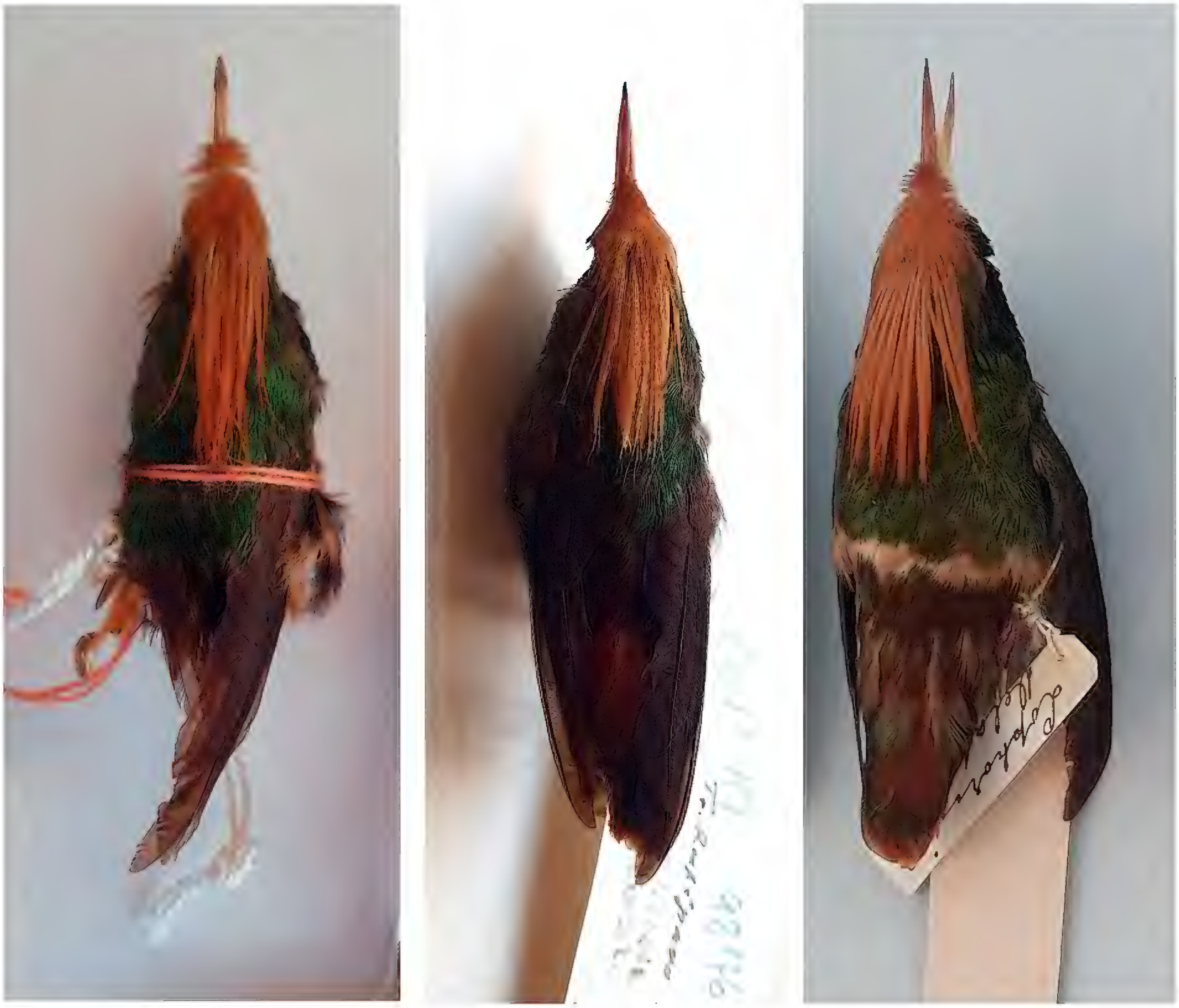

Fig. 5. Male specimens of *Lophornis d. lessoni* (left and middle, Colombia; Staatliches Museum für Naturkunde Stuttgart and Leibniz Institute for the Analysis of Biodiversity Change, Museum Koenig Bonn; and right, Panama; Natural History Museum, Tring): SMNS 30974, ZFMK Coll. Kl. 9876, and NHMUK unregistered (Guy M. Kirwan).

As a result, contra Walters' (1997) text but consistent with the NHMUK specimen that Walters apparently thought might be similar to those Floericke had described, we believe that *melaniae* can be referred to *L. stictolophus*, not *L. delattrei*. Three further considerations support this conclusion. First, the possibility that *melaniae* was collected in Colombia, where *L. delattrei lessoni* typically shows no or very little dark spotting on the crest, significantly reduces the chance of it being referable to this latter taxon. Second, Walters' (1997) speculation (repeated by Züchner 1999a), that the Stuttgart skins might have been unusually faded is not borne out by our investigation. Third, with the availability of many more specimens and photographs of live birds, Floericke's suggestion that *melaniae* was somewhat "intermediate" can also be discounted, as the characters of the crest (which is the only feature useful to separate males of the two species) fit within the range of variation exhibited by *L. stictolophus*, albeit perhaps only rarely; thus although the possibility that *melaniae* is of hybrid origin (already mentioned on the oldest labels attached to both syntypes) cannot entirely be excluded, it seems very remote. This is because known areas of overlap between the two relevant species are at most very few, for example, none has been found in northern Peru, despite the apparent proximity of the two species' ranges there (Schulenberg et al. 2007) and there appear to be no localities in Colombia with records of both species, for example, on eBird (https://ebird.org/), despite some distributional overlap on the maps in Hilty & Brown (1986) and Hilty (2021). Both these latter works emphasise that the distribution of *L. stictolophus* is largely restricted to elevations below that of *L. delattrei* in Colombia. Indeed, the only specific locality we have discovered with 'records' of both species is Jatun Sacha Biological Reserve, Napo province (01°04'S, 77°36'W), in eastern Ecuador,

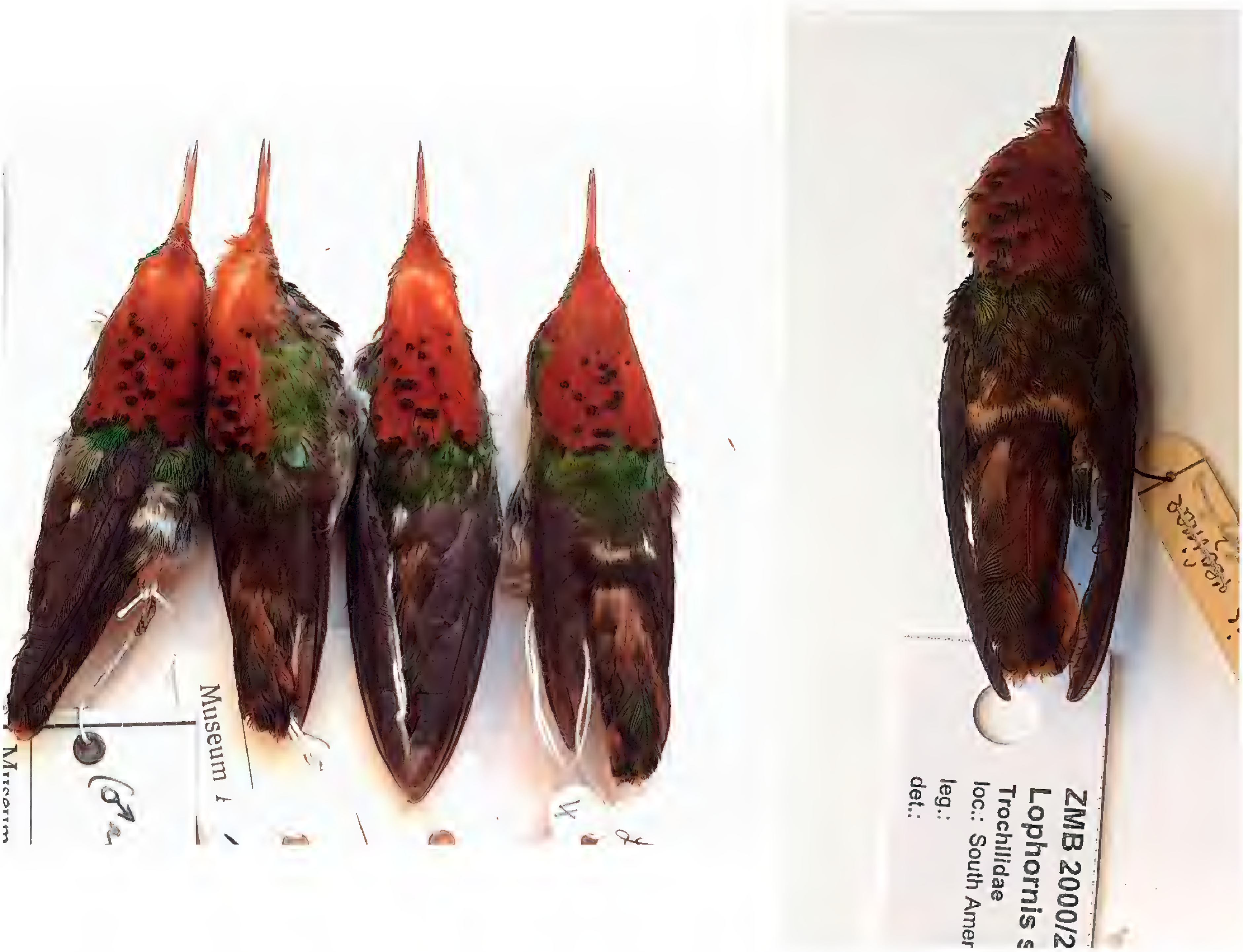

Fig. 6. Male specimens of *Lophornis stictolophus* (left-hand four at Leibniz Institute for the Analysis of Biodiversity Change, Museum Koenig Bonn; right-hand bird at Museum für Naturkunde, Berlin) (Guy M. Kirwan).

where *delattrei* has been claimed once, in April 1992, and *stictolophus* has been observed at least a few times (Ridgely & Greenfield 2001). *Lophornis delattrei* is still treated as of only hypothetical occurrence in Ecuador, based on the uncorroborated sighting at Jatun Sacha (Freile & Restall 2018), which at 400 m is below the usual elevational range of that species (Hilty & Brown 1986; Züchner 1999a; Schulenberg et al. 2007; Herzog et al. 2016). Our identification accords with the museum's own attribution to SMNS 30966.

Inevitably in cases like this where the identity of a museum specimen cannot be completely resolved by examination and comparison with other material, we recommend that a molecular study be undertaken on Floericke's two *melaniae* in the hope of a more certain conclusion.

Acknowledgements. We are grateful to Friederike Woog for providing access for GMK to study specimens at the Staatliches Museum für Naturkunde Stuttgart. Comparative material of other *Lophornis* taxa was examined at the Natural History Museum, Tring, thanks to Mark Adams and Hein van Grouw; at the Museum für Naturkunde, Berlin, due to the help of Pascal Eckhoff; and at the Leibniz Institute for the Analysis of Biodiversity Change, Museum Koenig, Bonn, through the kindness of Till Töpfer. Isabelle Weiss kindly assisted with translating the original description of *Lophornis melaniae*. Cat O'Carroll assisted with access to Mitteilungen über die Vogelwelt. Two referees and the subject editor, Till Töpfer, critiqued the submission.

REFERENCES

Dickinson EC, Remsen JV (eds) (2013): The Howard and Moore complete checklist of the birds of the world. Vol. 1. Fourth edn. Aves Press, Eastbourne

Eck S, Fiebig J, Fiedler W, Heynen I, Nicolai B, Töpfer T, van den Elzen R, Winkler R, Woog F (2011): Measuring birds [Vögel vermessen]. Christ Media Natur, Minden

Floericke C (1920): Systematisches. III. Neue Kolibriformen. Mitteilungen über die Vogelwelt 19: 2–3

Freile J, Restall R (2018): Birds of Ecuador. Helm, London

Gebhardt L (2006): Die Ornithologen Mitteleuropas: 1747 Bemerkenswerte Biographien vom Mittelalter bis zum Ende des 20. Jahrhunderts. Aula Verlag, Wiesbaden

Gould J (1846): On twenty new species of Trochilidae or humming birds. Proceedings of the Zoological Society of London 1846: 85–90

Gould J (1847): Drafts for a new arrangement of the Trochilidae, with the characters of two new genera and descriptions of three new species. Proceedings of the Zoological Society of London 1847: 94–96

Gould J (1855): A monograph of the Trochilidae, or family of hummingbirds. Vol. 3. Taylor & Francis, London

Gould J (1861): A monograph of the Trochilidae, or family of hummingbirds. Vol. 5. Taylor & Francis, London

Herzog SK, Terrill RS, Jahn AE, Remsen JV, Maillard O, García-Solíz VH, Macleod R, Maccormick, A, Vidoz JQ (2016): Birds of Bolivia. Field guide. Asociación Armonía, Santa Cruz de la Sierra

Hilty SL (2021): Birds of Colombia. Lynx Edicions, Barcelona

Hilty SL, Brown WL (1986): A guide to the birds of Colombia. Princeton University Press, Princeton

del Hoyo J, Elliott A, Sargatal J (eds) (1999): Handbook of the birds of the world. Vol. 5. Lynx Edicions, Barcelona

del Hoyo J, Collar NJ (2014): HBW and BirdLife International illustrated checklist of the birds of the world. Vol. 1. Lynx Edicions, Barcelona

Lesson RP (1832): Les Trochilidées ou des Colibris et les Oiseaux-Mouches. Arthus Bertrand, Paris

Lesson RP (1839): Oiseaux-mouches nouveaux ou très-rares, découverts par M. De Lattre dans son voyage en Amérique et décrits par MM. De Lattre et Lesson. Revue Zoologique, par la Société Cuvierienne 2: 13–20

Meyer de Schauensee R (1966): The species of birds of South America and their distribution. Academy of Natural Sciences, Philadelphia

Nehrkorn A (1910): Katalog der Eiersammlung, nebst Beschreibungen der Aussereuropäischen Eier. R. Friedländer & Sohn, Berlin

Peters JL (1945): Check-list of birds of the world. Vol. 5. Museum of Comparative Zoology, Cambridge, MA

Ridgely RS, Greenfield PJ (2001): The birds of Ecuador: status, distribution and taxonomy. Christopher Helm, London

Roselaar CS (2003): An inventory of major European bird collections. Pp. 253–337 in: Collar NJ, Fisher CT, Feare CJ (eds) Why museums matter: avian archives in an age of extinction. Bulletin of the British Ornithologists' Club 123A Supplement

Salvin O, Elliot DG (1873): On two species of Trochilidae of the genus *Lophornis*. Ibis (3)3: 279–280

Schifter H, Bauernfeind E, Schifter T (2007): Die Typen der Vogelsammlung des Naturhistorischen Museums Wien. Teil I. Nonpasseres. Kataloge der wissenschaftlichen Sammlungen des Naturhistorischen Museums in Wien 20, Aves, Heft 1. Naturhistorischen Museums Wien, Vienna

von Schreibers K (1833): Collectanea ad faunam Brasiliae. Collectanea ad Ornithologiam Brasiliae. Beyträge zur Vögelkunde Brasiliens. Neue Arten von Blumenspechten, Colibri. Strauß, Wien

Schulenberg TS, Stotz DF, Lane DF, O'Neill JP, Parker TA (2007): Birds of Peru. Christopher Helm, London

Simon E (1921): Histoire naturelle des trochilidés (synopsis et catalogue). Encyclopédie Roret, Paris

Vieillot LP (1817): Nouveau Dictionnaire d'Histoire naturelle, Tome 7. Chez Deterville, Paris

Walters M (1997): On the identity of *Lophornis melaniae* Floericke (Trochilidae). Bulletin of the British Ornithologists' Club 117: 235–236

Warren RLM (1966): Type-specimens of birds in the British Museum (Natural History). Vol. 1. British Museum (Natural History), London

Zimmer JT (1950): Studies of Peruvian birds. No. 57, The genera *Colibri*, *Anthracothorax*, *Klais*, *Lophornis*, and *Chlorestes*. American Museum Novitates 1463: 1–28

Züchner T (1999a): Rufous-crested Coquette *Lophornis delattrei*. Pp. 567–568 in: del Hoyo J, Elliott A, Sargatal J (eds) Handbook of the birds of the world. Vol. 5. Lynx Edicions, Barcelona

Züchner T (1999b): Spangled Coquette *Lophornis stictolophus*. P. 568 in: del Hoyo J, Elliott A, Sargatal J (eds) Handbook of the birds of the world. Vol. 5. Lynx Edicions, Barcelona

Bonn zoological Bulletin 72 (2): 209–222
2023 · Mondal S. et al.
https://doi.org/10.20363/BZB-2023.72.2.209

ISSN 2190–7307
http://www.zoologicalbulletin.de

Research article

urn:lsid:zoobank.org:pub:8B23DD35-D75A-4E7B-9501-F43147F94707

Some rare species of sea snakes (Squamata: Serpentes: Elapidae: Hydrophiinae: *Hydrophis, Microcephalophis*) from the Indian Coasts and nearby waters, lodged in major systematic Indian zoological collections

Sonia Mondal [1], **S.R. Ganesh** [2,*] **& C. Raghunathan** [3]

[1,3] *Zoological Survey of India, Herpetology Division, FPS Building, Indian Museum Complex, Kolkata, West Bengal, India*
[2] *Kalinga Foundation, Agumbe Hobli, Hosur Grama, Guddekere, Shivamogga-577411, Karnataka, India*
* *Corresponding author: Email: snakeranglerr@gmail.com*

[1] urn:lsid:zoobank.org:author:8E0D2E56-6060-4C77-B333-A08BF082B882
[2] urn:lsid:zoobank.org:author:F751BE54-F130-4196-A90A-D07A892EF912
[3] urn:lsid:zoobank.org:author:A7DAE65C-B49F-4A4B-BCD2-7C223003AB28

Abstract. Sea snakes of the genera *Hydrophis* Latreille *In* Sonnini & Latreille, 1801 and *Microcephalophis* Lesson, 1832 are also represented by some rare species in India and surrounding waters. Many species of Indian sea snakes are poorly known, except for some common species reported in marine faunal surveys. Here, based on a series of 107 specimens, we elaborate on nine such rare species of the genera *Hydrophis*, viz. *H. jerdoni* (Gray, 1849), *H. lapemoides* (Gray, 1849), *H. mamillaris* (Daudin, 1803), *H. nigrocinctus* Daudin, 1803, *H. stricticollis* Gunther, 1864, *H. viperinus* (Schmidt, 1852) and *H. obscurus* Daudin, 1803 as well as *Microcephalophis,* viz. *M. gracilis* (Shaw, 1802) and *M. cantoris* Gunther, 1864. We furnish data on the morphometrics and colouration in preservation for the above species based on material in the Zoological Survey of India, Kolkata (n=74) and the Bombay Natural History Society Museum, Mumbai (n=33). But for a few (n=19) specimens from Iran, Pakistan, Myanmar and Thailand for four species (*H. jerdoni, H. viperinus, H. obscurus, M. gracilis*), the vast majority of the examined specimens are from Indian coastlines. All material dealt with here are non-types, but include some historical specimens previously examined by European herpetologists. All species of *Hydrophis* and *Microcephalophis* represented here are those native to India. We also illustrate these seven species as preserved vouchers, all belonging to Indian material to further aid their future identifications.

Keywords. Arabian Sea, BNHS, colouration in preservation, scalation, sea snake, morphometry, Indian Ocean, Bay of Bengal, ZSI.

INTRODUCTION

Sea snakes are relatively poorly-represented groups of serpents in both Indian herpetological literature (Ganesh et al., 2019; see below) and Indian herpetological museums (Phipson 1888; Sclater 1891; Das & Chaturvedi 1998; Das et al. 1998; Das & Gayen 2004; Ganesh & Asokan 2010; Ganesh et al. 2020; Mondal et al. 2022). India has a diversity of 20 species of marine snakes, representing 18 species of true sea snakes belonging to the genera *Hydrophis* Latreille *In* Sonnini & Latreille, 1801 and *Microcephalophis* Lesson, 1832 (Ganesh et al. 2019). However, most studies that dealt with sea snakes in India, have time and again reported just a few handful common species. This is understandably so given the fact that they are inherently tough to sample, dependent on (often commercial) fishing vessels and also some climatic fluctuation factors. This limits the scope for active field sampling and collection including site-selection, time-duration of sampling, selective or species-specific retention and/or discordance of samples as per the research requirements of the academic fraternity involved. Thus, at least in India, the catches or collection sorties are wholly predicated upon the primary, non-aligning interests and motives of the vessels involved (Costello et al. 2010, 2017). Almost always, sea snakes are far from being the primary objective of such missions.

On the whole, literature on Indian sea snakes could be more or less grouped into the following kinds. First, classical 19th and 20th century taxonomic treatises, such as Gunther (1864), Theobald (1868, 1876), Phipson (1888), Boulenger (1890, 1896), Sclater (1891), Wall (1906, 1909) and Smith (1926, 1943). Second, post-Independence studies by Indian herpetologists in the later part of the 20th century (Ahmed, 1975; Murthy, 1977; Myers, 1947). Last, recent scholarship on the subject due to a renewed interest in biodiversity explorations of the country. Either they are in the form of single-species/

Received: 22.06.2023
Accepted: 20.11.2023

Corresponding editor: W. Böhme
Published: 28.11.2023

single-instance observations (e.g., Chandrasekar et al., 2018; John et al., 2015; Karthikeyan et al., 2008; Parmar, 2018, 2019a,b; Tripathy, 2006) or long-term studies (e.g., Lobo et al. 2004, 2005; Kannan & Rajagopalan 2008; Karthikeyan & Balasubramanian 2008; Padate et al. 2009; Damotharan et al. 2010; Jeyabaskaran et al. 2015; Muthukumaran et al. 2015; Venkatraman et al. 2015; Prachi & Ramesh 2016; Dabhi et al. 2019; Desouza & Rao 2021; Rao et al. 2021; Tambre et al. 2021).

This leads to two issues: (i) higher number of specimen-collections of some common sea snake species, (ii) more frequent reports of certain common species of sea snakes consequent upon such distorted collection missions/parties involved. However, despite the appreciably reasonable efforts put forth by Indian herpetologists in studying and sampling sea snakes in situ, this knowledge gap on other rarer sea snake species has only widened over time. In most cases, these species were merely cited in regional checklists and faunistic studies with little new knowledge coming in. Many recent regional treatises on Indian snakes (Daniel, 2002; Das, 2002; Whitaker & Captain, 2004) could not shed enough light on most of these species. This situation calls for a separate consolidation of data that has got a direct bearing especially on those few rare Indian sea snake species alone. Therefore after consulting publications and perusing museum collections, we cherry-picked seven obscure species of *Hydrophis* Latreille *In* Sonnini & Latreille, 1801 and two species of *Microcephalophis* Lesson, 1832. We subjected these species to descriptions and illustrations based on vouchered non-types from Indian and in a few exceptions, nearby waters so as to shed more light on these little-known species.

The following recent (post-1970) studies on sea snakes in the Indian coastline did not include any of the rarer sea snake species dealt with in this work. These include Murthy & Rao (1976, 1988), Kalaiarasan & Kanakasabai (1994), Lobo et al. (2004, 2005), Tripathi (2006), Kumar et al. (2007), Karthikeyan & Blasubramanian (2008), Karthikeyan et al. (2008), Padate et al. (2009), Palot & Radhakrishnan (2010), Jeyabaskaran et al. (2015), John et al. (2015), Muthukumaran et al. (2015), Venkatraman et al. (2015), Prachi & Ramesh (2016), Chandrasekar et al. (2018), Parmar (2018, 2019) and Tambre et al. (2020). Hence this study.

MATERIALS AND METHODS

This study is based on an examination of 107 preserved, non-type voucher specimens representing nine species of the genera *Hydrophis* Latreille *In* Sonnini & Latreille, 1801 and *Microcephalophis* Lesson, 1832 housed in India's leading natural history collections namely: Zoological Survey of India, Kolkata (ZSI, =74) and the Bombay Natural History Society Museum, Mumbai (BNHS, =33). A total of 17 characters including scalation, measurements and colour pattern were scored from these specimens. Morphometric landmarks, terminologies and method of scoring follow Mondal et al. (2022). Ventrals were counted following Dowling (1951). Examinations were done using LEICA EZ4 model microscopes and photographs of the subject were taken using Nikon D700 model high-resolution digital cameras.

RESULTS

Hydrophis jerdonii (Gray, 1849)
(Fig. 1, Table 1)

Materials examined (n=14). INDIA: ZSI 21819, Mouth of the Arasalar river, Karaikkal, Tamil Nadu, coll. 28.12.1956; ZSI 22477, Gopalpur, Ganjam district, Odisha, coll. G. Ramakrishna 28.12.1962; ZSI 28229, Bay of Bengal, coll. Dr Walsh 20.05.1890; BNHS 2282 (2 ex.), Madras (= Chennai), coll. Frank Wall 31.12.1907; MYANMAR: ZSI 8237, Mergui, Coll. W. Theobald; ZSI 11486-9, Mergui, coll. Dr Anderson, 18.01.1892; THAILAND: ZSI 18579, Patani Bay, Siamese-Malay Strait, coll. Dr N. Annandale; ZSI 18581-83, Singgora, Siam, coll. Dr N. Annandale, January 1916.

Description and Variation. Head short, snout narrowed anteriorly, rostral higher than broad; nostril superior, nasals in contact with each other; prefrontal small, in one specimen triangular (BNHS 2282), not in contact with 2nd supralabial; frontal longer than the distance from the rostral; parietal longer than broad; single anterior temporal, often 6th supralabial fused with temporal; one supraocular on each side of head; one preocular on each side of head; one postocular on each side of head; 6 supralabials on each side of the head, sometimes 5, 3rd and 4th touching the eye, 6th fused with temporal; 6–7 infralabials, rarely 5, 3 infralabials touching chin shield; Chin shield well developed, both the pairs in contact with each other, anterior pair is smaller than the posterior pair; scales around neck 17, rarely 18, only one specimen with 16 (ZSI 18579); scales around midbody 19–22, only one specimen with 23 (ZSI 18582); ventral 214–258, twice the size of the adjacent dorsal scale, posteriorly narrow; preanal slightly enlarged; dorsal scale with single keel; number of bands around the body 30–43, 2–4 bands on tail, one specimen without banding (BNHS 2282); head length 12.1–24.1 mm; head width 4.9–10.7 mm; head depth 4.0–7.6 mm; snout-vent length 375.0–958.0 mm; tail length 50.0–110.0 mm. Dorsum olive grey colour with dark grayish black bands across the body, ventral creamy yellow, tail creamy yellow with dark grayish black bands. Head olive grey dorsally, lower labial creamy white.

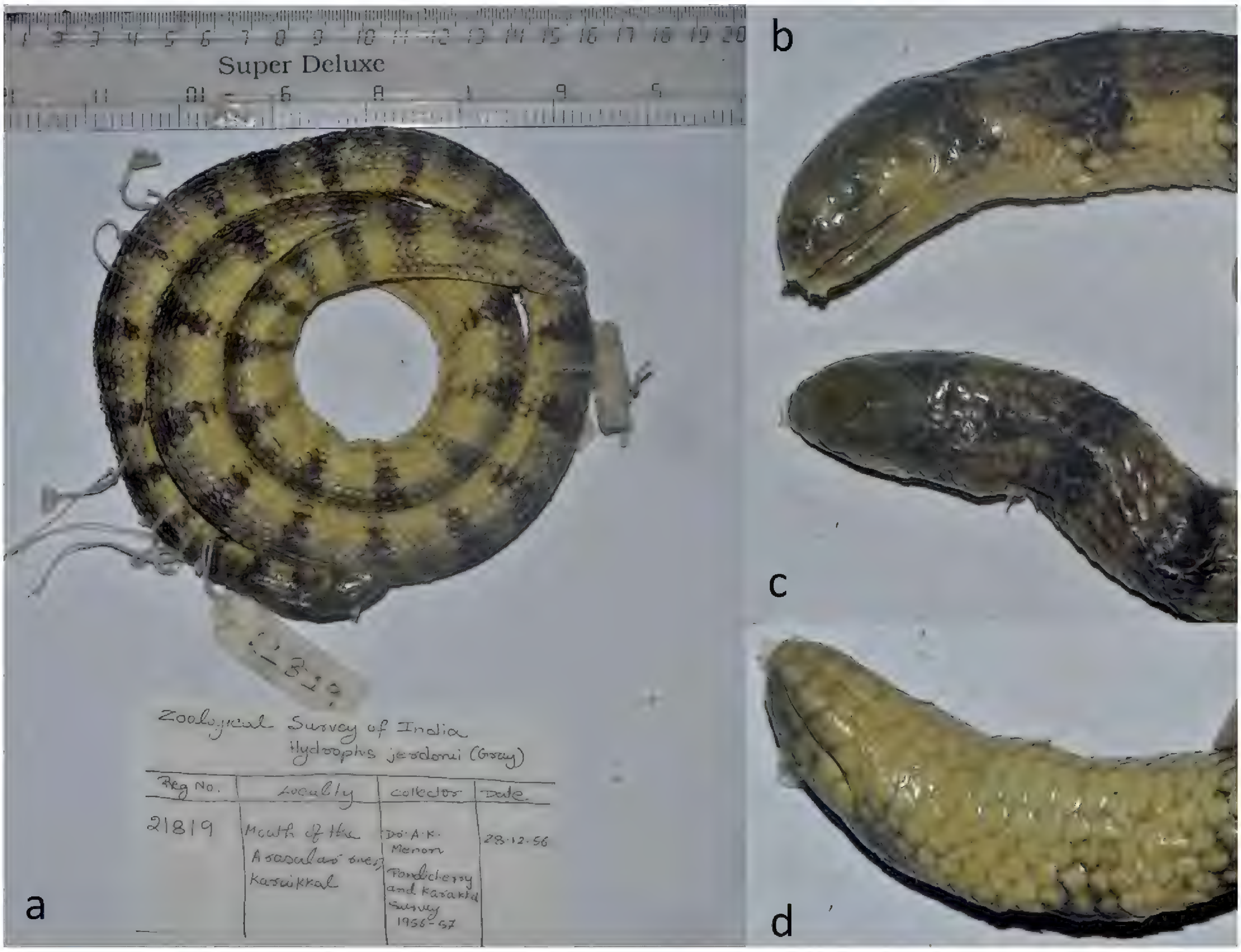
Super Deluxe
Zoological Survey of India
Hydrophis jerdoni (Gray)
Reg No. | Locality | collector | Date
21819 | Mouth of the Arasalar river, Karaikkal | Dr. A. K. Menon Pondicherry and Karaikal Survey 1956–57 | 28.12.56
a
b
c
d

Fig. 1. *Hydrophis jerdoni* (ZSI 21819). **A**. Entire. **B**. Head lateral. C. Head dorsal. D. Head ventral profiles. Photo: Sonia Mondal.

Hydrophis lapemoides (Gray, 1849)
(Fig. 2, Table 1)
Materials examined (n=4). INDIA: ZSI 27936, Tamil Nadu, coll. C.H. Satyanarayanan etc., 24.09.2003; BNHS 3357–58, Ervady, Gulf of Mannar, coll. Aaron Lobo 25.06.2005; PAKISTAN: ZSI 8632, Persian Gulf at Gwadar, Coll. Not Known.

Description and Variation. Head moderate, rostral broader than high, rarely higher than broad (ZSI 27936); nostril superior, nasal in contact with each other; prefrontal elongated, in contact with 2nd supralabial; frontal longer than the distance from the rostral; parietal longer than wide; single anterior temporal or 1+2; one supraocular on each side of head; one preocular on each side of head; 2–3 postocular on each side of head; 7–8 supralabials on each side of the head, 2nd supralabial touching prefrontal, 3rd and 4th touching the eye, sometimes 3rd, 4th & 5th touches the eye (ZSI 8632), 4th, 5th and 6th sometimes broken, last scales small; 8–9 infralabials on each side of the head, 3–4 infralabials touching chin shield, cuneate scale present between 3rd & 4th infralabial (ZSI 8632); chin shield well developed and in contact with each other or sometimes posterior pair separated by 1–2 scales, anterior pair larger than posterior pair; scales around the neck 29–31; scales around midbody 39–41; ventrals 310–345, distinct throughout, slightly larger than the adjacent dorsal scales, posterior narrow; preanal enlarged; dorsal scale with single keel; number of bands around the body 37–58 as rhomboidal spots, 2–5 bands on the tail; head length 20.3–23.9 mm; head width 7.0–12.0 mm; head depth 8.3–8.7 mm; snout–vent length 643.0–863.0 mm; tail length 68.0–88.0 mm. Dorsum light reddish brown with dark greyish black bands till tail. Head reddish brown with black mark on frontal and parietals, lower labial brown.

Hydrophis mamillaris Daudin, 1803
(Fig. 3, Table 1)
Materials examined (n=7). INDIA: ZSI 13392, Bay of Bengal, coll. Dr Walsh 20.05.1890; ZSI 19481, Gulf of Cambay, coll. S. T. William Carrick December, 1921; ZSI 22671 Digha beach on way to Paddapur, Midnapur district, West Bengal, coll. Dr A. K. Dutta 04.09.1964; BNHS 2329 (2 ex.), Mumbai, Maharashtra

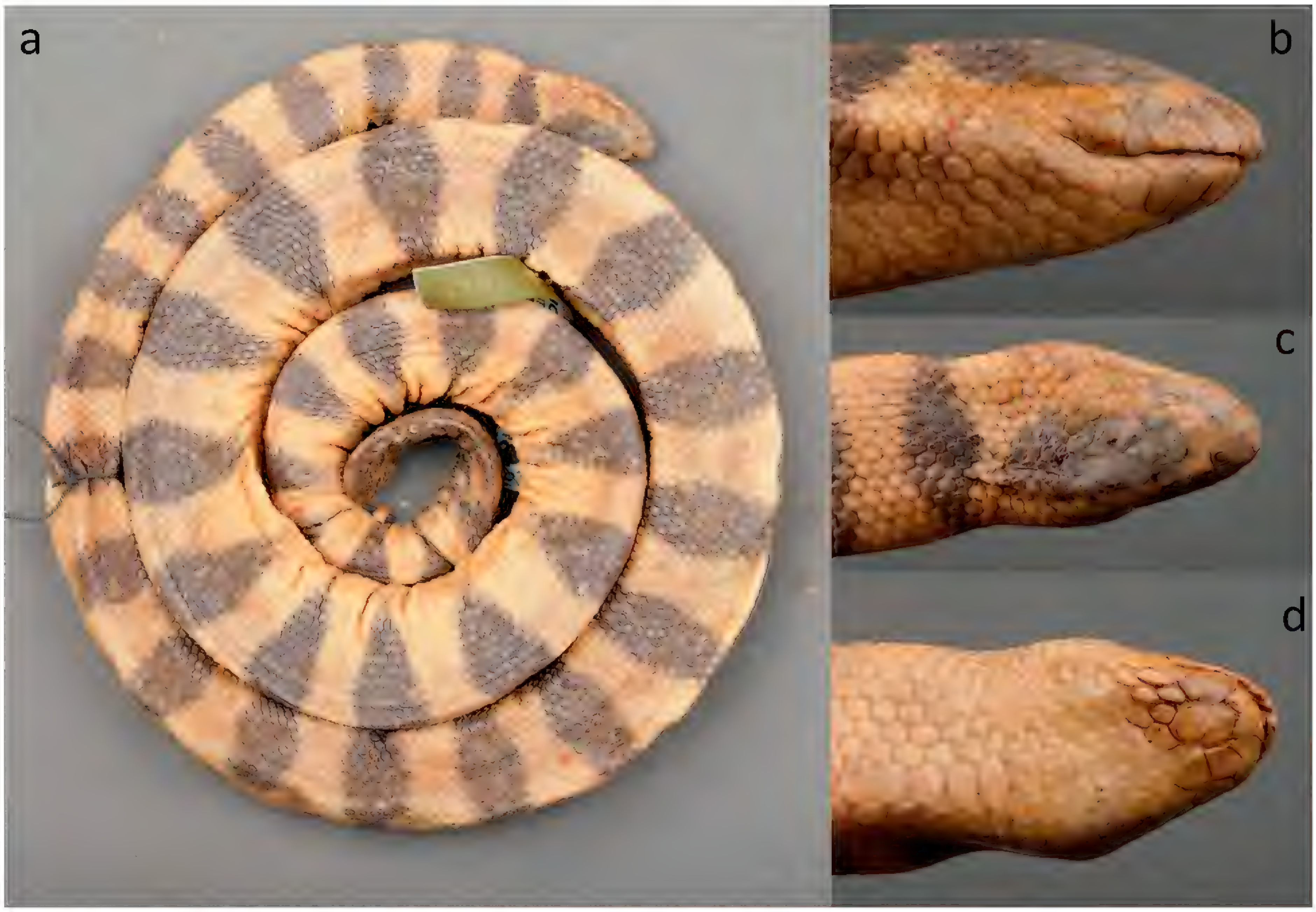

Fig. 2. *Hydrophis lapemoides* (BNHS 3358). **A**. Entire. **B**. Head lateral. **C**. Head dorsal. **D**. Head ventral profiles. Photo: O.D. Adhikari.

coll. 31.12.1907; BNHS 2330, Alibaug, Raigad district, Maharashtra, coll. W.O. Alcock 01.07.1917; BNHS 2331 Kihim, Alibaug, Raigad district, Maharashtra, coll. Humayun Abdulali.

Description and Variation. Head small; rostral broader than high; nostril superior, nasal in contact with each other; prefrontal slightly elongated or triangular, in contact with 2nd supralabial (in one specimen prefrontal fused with nasal, ZSI 13392); frontal longer than the distance from the rostral; temporals 2+2, two specimens with only one anterior temporal (ZSI 19481 and ZSI 13392); one supraocular on each side of head; 1–2 preocular on each side of head; 1–2 postocular on each side of the head; 6–7 supralabials, 2nd touching the prefrontal, 3rd and 4th touching the eye (one specimen 3rd–5th touching the eye, BNHS 2329), sometimes 5th and 6th broken; 7–8 infralabials, 3–4 infralabials touching chin shields; chin shields well developed, both the pairs in contact with each other, one specimen where both the chin shields were separated from each other (ZSI 22671); scales around the neck 25–30; scales around the midbody 33–45; ventrals 260–350, distinct throughout, anteriorly scales larger than the adjacent dorsal scale, posteriorly narrow; preanal small; dorsal scale with no keels or feeble keeling; number of bands around the body 40–55; 2–9 bands on the tail; head length 12.8–17.4 mm; head width 5.4–7.0 mm; head depth 4.2–6.9 mm; snout-vent length 355.0–743.0 mm; tail length 35.0–80.0 mm. Dorsum light whitish grey ground colour with dark black bands across the body, ventral creamy interrupted by dark bands, tail black ventrally and posterior part, anteriorly same ground colour and banding as dorsal body. Head dark black with a streak of white mark across the supraocular and temporals, lower labial grey.

Hydrophis nigrocinctus Daudin, 1803

(Fig. 4, Table 1)

Materials examined (n=3). INDIA: ZSI 24084 Bidhya river, Sunderban, 24 Parganas, West Bengal, coll. N.C.Gayen, 20.09.1983; UNKNOWN: ZSI 8239-40 no data.

Description and Variation. Head moderate; rostral higher than broad, visible from dorsal view of head; nostril superior, nasals in contact with each other; prefrontal squarish, not in contact with 2nd supralabial; frontal longer than the distance from the rostral; parietal longer than broad; temporals 2+3; one supraocular on each side of head; 1–2 preocular on each side of the head, one specimen with a scale present in between the prefrontal and nasal just above the 2–3 supralabials, on only one side of head; 2 postocular on each side of the head; 7 supra-

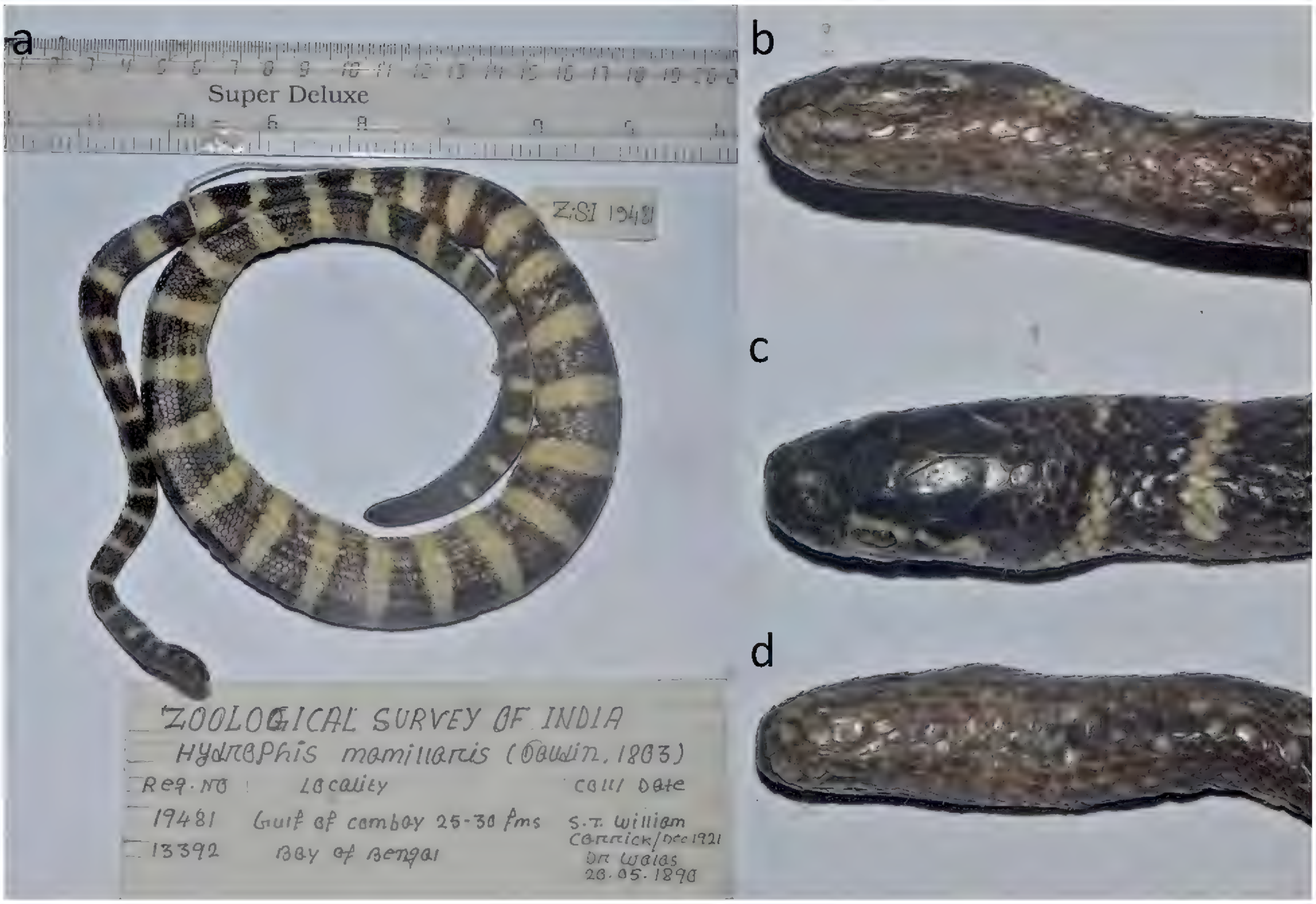
a
b
c
d
Super Deluxe
Z.SI 19481
ZOOLOGICAL SURVEY OF INDIA
Hydrophis mamillaris (Dauwin, 1803)
Reg. No Locality Coll Date
19481 Gulf of comboy 25-30 fms S.T. William Carrick/Dec 1921
13392 Bay of Bengal Dr Walas 20.05.1890

Fig. 3. *Hydrophis mamillaris* (ZSI 19481). **A**. Entire. **B**. Head lateral. **C**. Head dorsal. **D**. Head ventral profiles. Photo: S. Mondal.

labials, 4th touching the eye; 7–8 infralabials, 3 infralabials touching the chin shields, cuneate scales present between 2nd and 3rd or after 3rd infralabial; chin shields well developed, anterior pair in contact with each other, Posterior pair separated from each other; scales around the neck 27–30; scales around the midbody 36–42; ventrals 300–332, distinct throughout, not twice as broad as the adjacent dorsal scales; preanal slightly enlarged; dorsal scale with single keel; number of bands around the body 54–56, 6–10 bands on the tail; head length 12.9–27.3 mm; head width 4.3–12.3 mm; head depth 4.0–8.8 mm; snout-vent length 460.0–1105.0 mm; tail length 53.0–135.0 mm. Dorsum olive light brown ground colour with dark brown narrow bands, ventral light yellow colour , tail light brownish yellow with dark bands. Head olive brown with brown markings on the prefrontal, frontal and parietals, lower labial creamy yellow.

Hydrophis stricticollis Günther 1864
(Fig. 5, Table 1)

Materials examined (n=3). INDIA: ZSI 8254, 8256 Hooghly, West Bengal, coll. H.L. Haughton; ZSI 23737, Gopalpur, Ganjam district, Odisha, coll. Dr M. Hafizullah 24.11.1977.

Description and Variation. Head small, rostral broader than high, nostril superior, nasal in contact with each other; prefrontal slightly elongated, in contact with 2nd supralabial; frontal longer than or shorter than the distance from the rostral; parietal longer than broad; single anterior temporal or 1+2; one supraocular on each side of head; one preocular on each side of head; 1–2 postocular on each side of head; 7 supralabials, 2nd in contact with prefrontal, 3rd and 4th touching the eye, last scales small; nine infralabials, 3 infralabials touching anterior chin shield, cuneate scales present, last scale small; chin shield well developed, both the pair in contact with each other, in one specimen posterior pair separated by a single scale (ZSI 8256); scales around neck 32–39; scales around midbody 44–46; ventrals 378–451, district throughout, not twice as broad as the adjacent dorsal scales; preanal small; bands around the body is distinct in one specimen, with 44 bands, in another specimen anterior half of the body have 46 bands with posterior body with uniform dorsum colour and third specimen with faint diffused bands; head length 19.3 mm; head width 7.6 mm; head depth 7.3 mm; snout-vent length 890.0–955.0 mm; tail length 90.0–130.0 mm. Dorsum olive brown ground colour with feeble slightly darker bands visible anteriorly, tail olive brown interrupted with darker brown bands. Head olive brown, lower labial cream in colour.

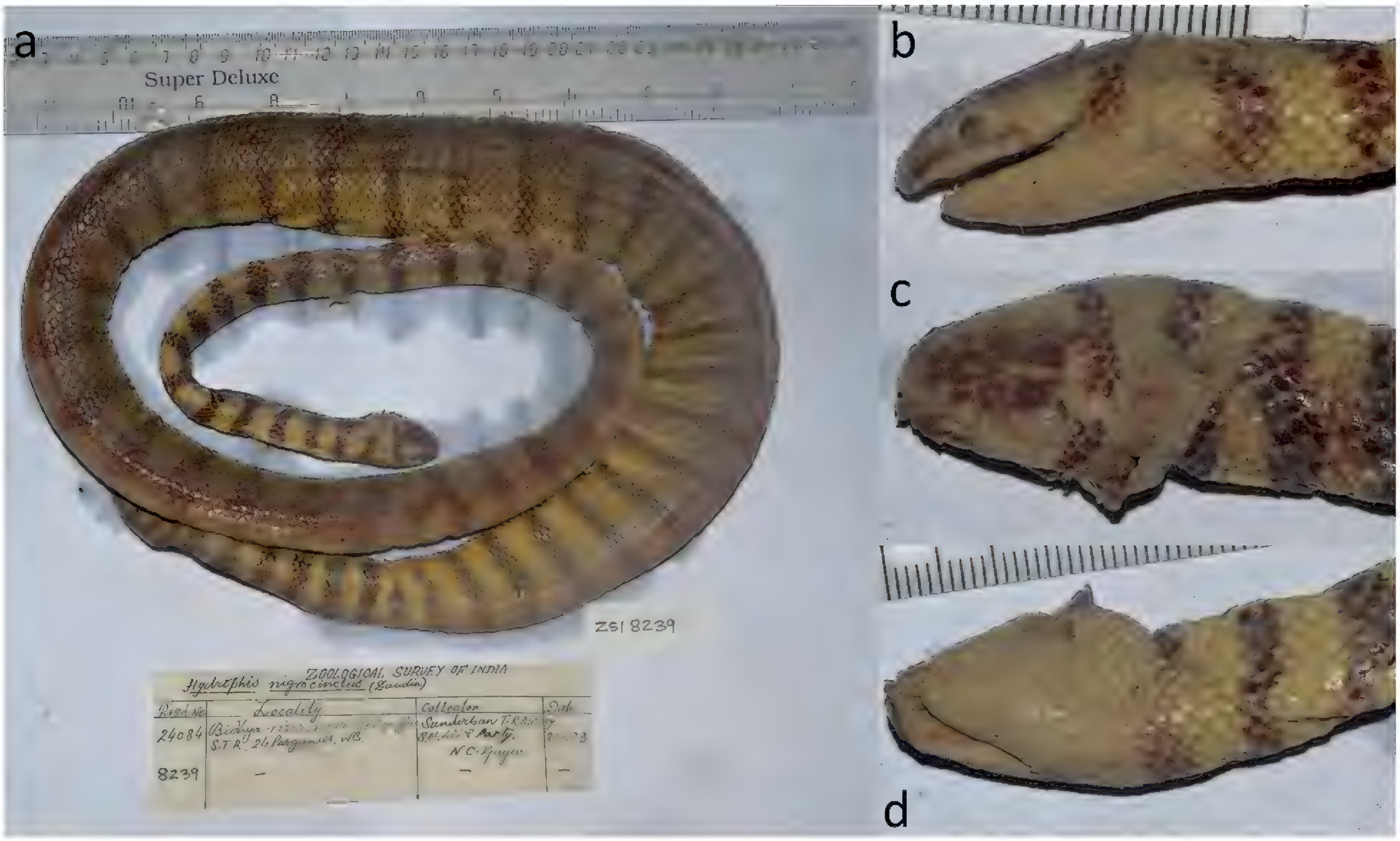

Fig. 4. *Hydrophis nigrocinctus* (ZSI 82399). **A**. Entire. **B**. Head lateral. **C**. Head dorsal. **D**. Head ventral profiles. Photo: S. Mondal.

Hydrophis viperinus (Schmidt, 1852)
(Fig. 6, Table 1)
Materials examined (n=14). INDIA: ZSI 8274 Puri, Odisha, coll. October, 1971; ZSI 8277, Puri, Odisha, coll. Dr Fayrer, October, 1871; ZSI 13594 Ganjam coast, Odisha, coll. A. Neurham; ZSI 14481 Puri, Odisha, coll. D.I.L.Hendley; ZSI 16376 Puri, Odisha, coll. J.Ircurs Jenkins; ZSI 19209 Puri, Odisha Coast, coll. Dr B. Prashad 18.10.1919; ZSI 22650 Digha, West Bengal, coll. Dr A.K. Dutta 03.09.1964; ZSI 22651 Karwar shore, Mysore State, coll. Dr Ummur Kutty & B. Sinha 16.01.1967; BNHS 2284 Madras (= Chennai), Tamil Nadu, coll. Frank Wall 31.12.1907; BNHS 2285 Karwar, Uttar Kannada district, Karnataka coll. C.C. Boyd 31.12.1907; BNHS 2286 Odisha coast, coll. Charles Bailey 01.03.1915; BNHS 3362 Mandapam, Gulf of Mannar, Ramanathapuram district, Tamil Nadu, coll. Aaron Lobo 11.01.2005; BNHS 3413 Off Sinquirim-Baga beach, Goa, coll. Aaron Lobo 22.01.2003. MYANMAR: ZSI 11497 Mergui, 7 miles from land, coll. Dr Anderson 16.01.1892.

Description and Variation. Head short, depressed, snout broadly rounded; rostral broader than high, nostril superior, nasal in contact with each other; prefrontal triangular, small, not in contact with supralabial; frontal longer than or smaller than the distance from the rostral; parietal longer than broad; 2 anterior temporals, sometimes 1+2, rarely one anterior temporal (BNHS 3413 and 3362); one supraocular on each side of head; one preocular on each side of head, in one specimen single scale present between preocular and nasal (BNHS 2284); 1–2 postocular on each side of head; 7–8 supralabials, 2nd largest, 3rd–5th touching the eye or only two of them touching the eye; 7–9 infralabial, 3–4 infralabials touching the chin shields, cuneate scales present sometimes; chin shields well developed, both the pairs in contact with each other or anterior pair in contact with each other and posterior pair separated, rarely both the pairs separated, posterior pair larger than the anterior pair; scales around neck 28–33; scales around midbody 41–48; ventrals 225–266, distinct throughout, anteriorly more than twice larger than adjacent dorsal scale, broader, posterior narrow; preanal slightly enlarge; dorsal scale with single dorsal keel; bands around the body absent giving a uniform grey colour of the dorsum or sometimes rhomboidal bands present prominent along the later side, number of bands varies from 18–33 when present; head length 13.9–25.0 mm; head width 7.2–12.5 mm; head depth 4.6–9.3 mm; snout-vent length 260.0–679.0 mm; tail 38.0–83.0 mm. Dorsum uniform grey colour without bands, ventral creamy white, tail entirely black without any bands. Head dorsum uniform grey colour, upperlabial and lower labial creamy white.

Hydrophis obscurus Daudin, 1803
(Fig. 7, Table 1)
Materials examined (n=30). INDIA: ZSI 8253 Mouth of River Hooghly, West Bengal, coll. H.L. Haughton;

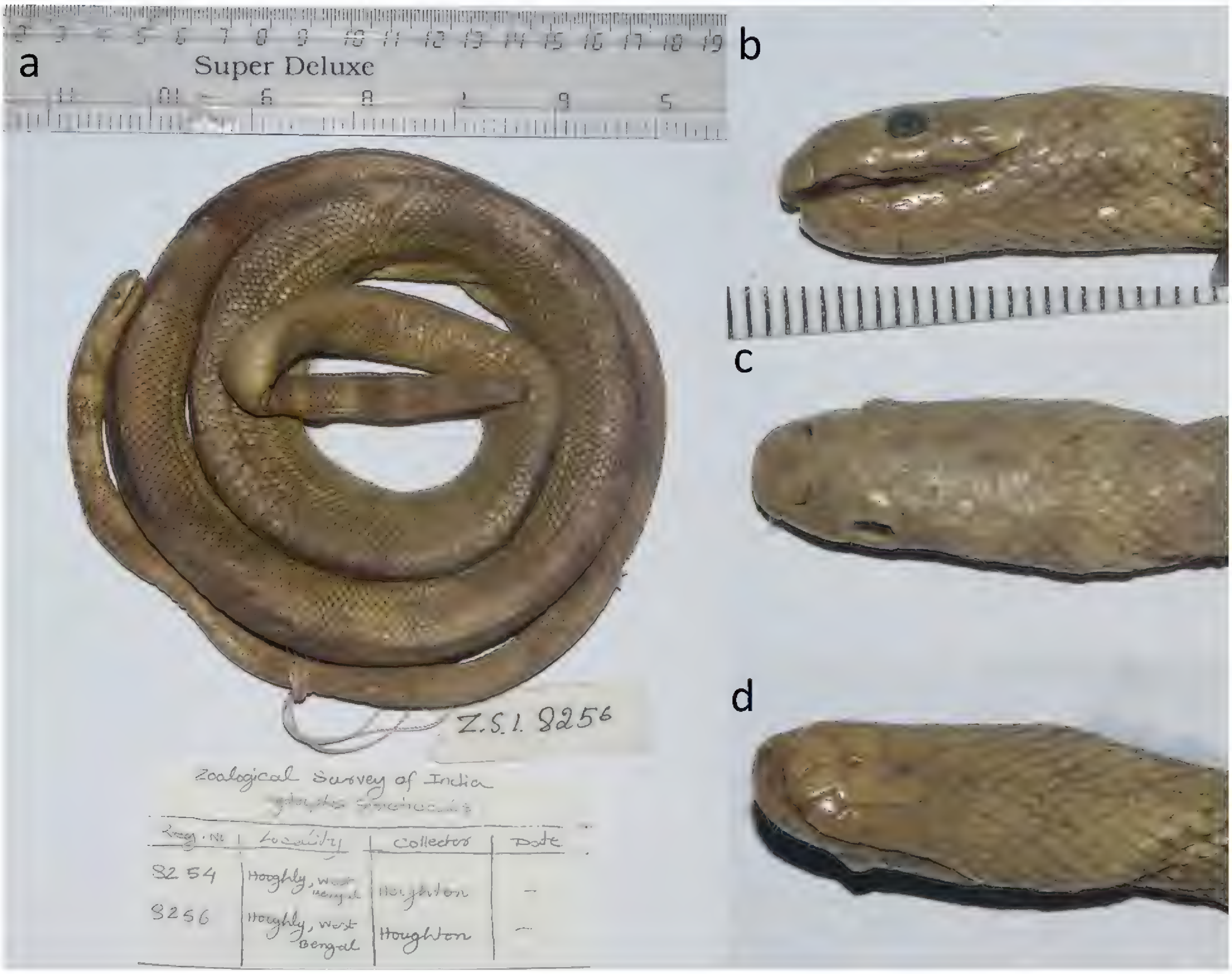
a
Super Deluxe
b
c
d
Z.S.I. 8256
Zoological Survey of India
Reg. No | Locality | Collector | Date
8254 | Hooghly, West Bengal | Houghton | –
8256 | Hooghly, West Bengal | Houghton | –

Fig. 5. *Hydrophis stricticollis* (ZSI 8256). **A**. Entire. **B**. Head lateral. **C**. Head dorsal. **D**. Head ventral profiles. Photo: S. Mondal.

ZSI 8255 Hooghly River, West Bengal, coll. Dr Anderson 1866; ZSI 17531-17534, 17538 Chilka Lake, Odisha; ZSI 17341-17345 Chilka Lake, Odisha, coll. Dr N. Annandale 21–31.07.1913; ZSI 18003-18010 Chilka Lake, Odisha; ZSI 20677 3/2 miles southeast of Bagauipara, Sunderban, coll. June 1929; BNHS 2320 (2 ex.) Karwar, Uttar Kannada district, Karnataka, coll. C.C.Boyd 31.12.1907; BNHS 2319 (4 ex.) Chilka Lake, Odisha, coll. H.W.Weslls; MYANMAR: ZSI 11496 Mergui, coll. Dr Anderson, 20.01.1892; UNKNOWN: BNHS 2321 (2 ex.) no data.

Description and Variation. Head small, rostral broader than high; nostril superior, nasal in contact with each other; prefrontal slightly elongated, in contact with 2nd supralabial; frontal smaller than the distance from the rostral, in one specimen the frontal is as long as the distance from the rostral (BNHS 2321); parietal longer than broad; single anterior temporal; one supraocular on each side of head; one preocular on each side of head, in one specimen preocular fused with prefrontal (BNHS 2320); one postocular on each side of the head; 6–7 supralabial, 2nd touching prefrontal, 3rd and 4th touching the eye; 6–8 infralabials, 3–4 infralabial touching the chin shield; chin shields well developed, anterior pair in contact with each other, posterior pair separated from each other or sometimes both the pairs in contact with each other, posterior pair larger than the anterior pair; scales around the neck 19–23; scales around midbody 26–32; ventrals 264–363, not twice as broad as the adjacent dorsal scales; preanal small, specimens of BNHS have slightly larger; number of bands around the body 45–69; 2–9 bands on the tail; head length 9.1–16.1 mm; head width 3.1–6.7 mm; head depth 2.5–6.4 mm; snout-vent length 395.0–1245.0 mm; tail 43.0–140.0 mm. Dorsum light grey ground colour with dark brown bands across the body, ventral brown, tail light grey with dark banding. Head dark brown dorsally with creamy white spots across the postocular to parietals and triangle shaped mark on the nasal and prefrontal, lower labial brown.

Microcephalophis gracilis (Shaw, 1802)
(Fig. 8, Table 1)

Materials examined (n=22). INDIA**:** ZSI 8268 Hooghly, West Bengal, H.L.Haughton; ZSI 11460 and 11461

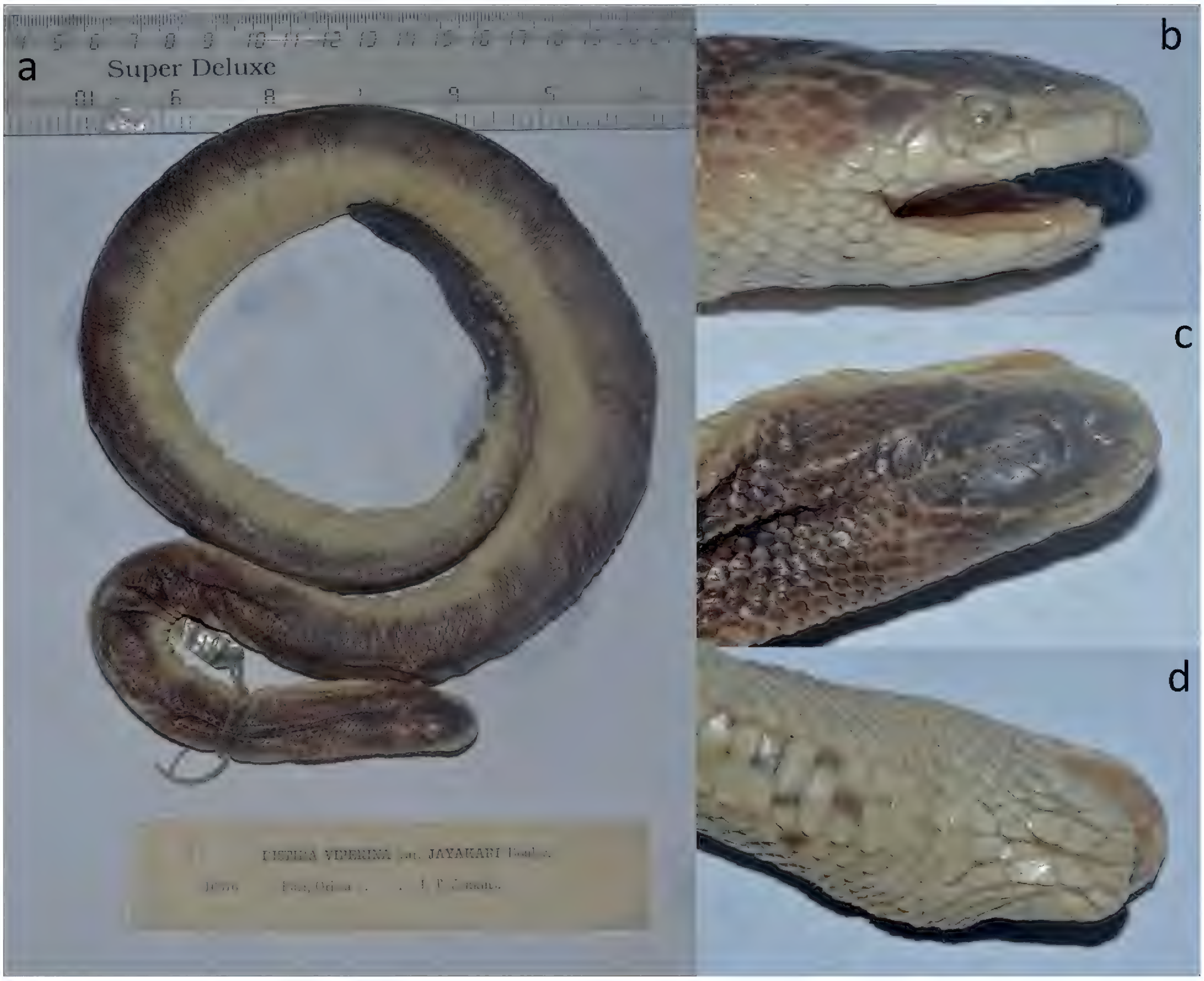

Fig. 6. *Hydrophis viperinus* (ZSI 16376). **A**. Entire. **B**. Head lateral. **C**. Head dorsal. **D**. Head ventral profiles. Photo: S. Mondal.

Puri, Odisha; ZSI 16549 Puri, Odisha, coll. B. Paira; ZSI 21825 Tranquebar (now Tharangambadi), Tamil Nadu, coll. A.G.K. Menon on 28.12.1956; ZSI 21826 Kalingimedu, Karaikkal, Tamil Nadu, coll. on 11.02.1957; ZSI 22521 and 22522 Sand head mouth of Hooghly, West Bengal, coll. P.V. Lady Fraser, in 1924; ZSI 22673 Digha beach on way to Paddapur, dist. Midnapur, West Bengal, coll. Dr A. K. Dutta on 03.09.1964; BNHS 2364 and 2365 Madras, Tamil Nadu, coll. Maj. F.Wall, on 31.12.1907; BNHS 2367, Alibaug, Raigad, Mumbai, Maharashtra, coll. W.O. Alcock, on 01.07.1917; BNHS 2368 Mumbai, Maharashtra; BNHS 3364 Pamban, Gulf of Mannar, Tamil Nadu, coll. Aaron Lobo on 07.01.2005; MYANMAR: ZSI 11484 Mergui (= Myeik), coll. Dr Anderson, on 20.01.1882; PAKISTAN: ZSI 8468 Persian Gulf at Gwadar, Baluchistan, coll. W.J. Blanford in 1872; ZSI 8543 Karachi, Pakistan, coll. Karachi museum; IRAN: BNHS 2359 Persian Gulf, coll. W.F.Townsend, on 31.12.1907; BNHS 2360, same as above, coll. on 01.01.1914; BNHS 2361 (2 ex), Chabahar, Persian Gulf, coll. Capt. J.E.B. Hotson, on 21.03.1917; BNHS 2362, Jask, Persian Gulf, Hormozgan province, coll. Maj. K.G. Gharpurey, coll. 22.02.1918.

Description and Variation. Head very small, elongate, body long with slender anteriorly and thick compressed posteriorly; snout projecting beyond the lower jaw; rostral broader than high, except in one specimen with higher than broad (BNHS 2364), extending well on to the upper surface of the snout; prefrontal slightly elongated, touching the 2nd supralabial; frontal shorter than the distance from the rostral; parietal longer than broad; single anterior temporal, one example 1+2 (ZSI 14467); one supraocular on each side of head; one preocular on each side of head; one postocular on each side of head, rarely 2; 6 supralabial on each side of the head, 3rd and 4th touching the eye; 7 infralabials, 4 infralabials touching chin shield; chin shield well developed, both the pairs in contact with each other, anterior pair is smaller than the posterior pair, in one specimen anterior pair is larg-

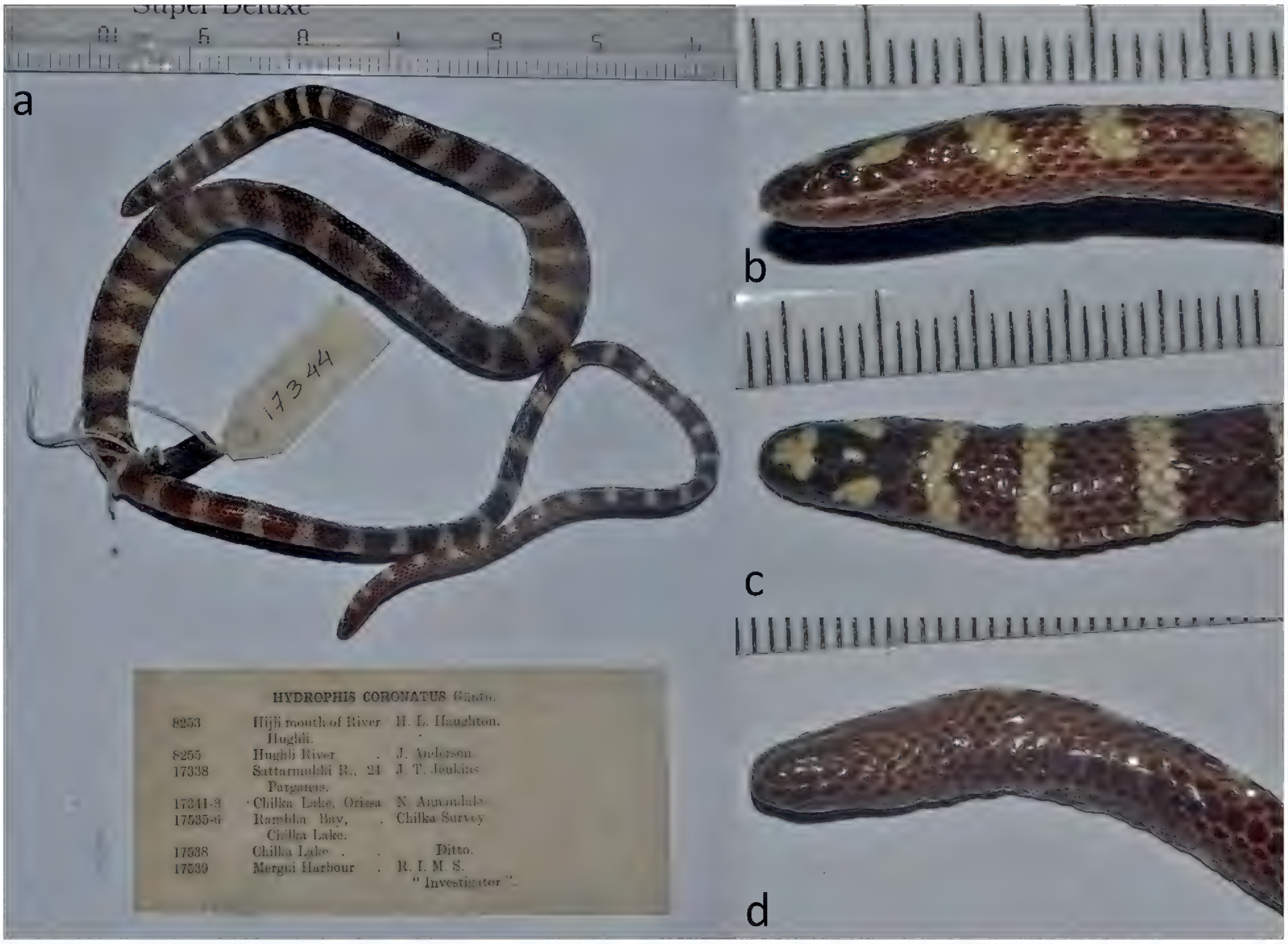
Super Deluxe
a
17344
HYDROPHIS CORONATUS Günth.
8253 Hijli mouth of River Hughli. H. L. Haughton.
8255 Hughli River . J. Anderson
17338 Sattarmukhi R., 24 Parganas. J. T. Jenkins
17341-3 Chilka Lake, Orissa N. Annandale
17535-6 Rambha Bay, Chilka Lake. . Chilka Survey
17538 Chilka Lake . . Ditto.
17539 Mergui Harbour . R. I. M. S. "Investigator".
b
c
d

Fig. 7. *Hydrophis obscurus* (ZSI 17344). **A**. Entire. **B**. Head lateral. **C**. Head dorsal. **D**. Head ventral profiles. Photo: S. Mondal.

er than posterior pair (BNHS 2367); scales around neck 19–20, in one specimens 17 (BNHS 2368), in another single specimen 21 (ZSI 16549); scales around midbody 27–38; ventrals 228–285, distinct from adjacent dorsal scale, posteriorly divided by a median furrow into two ; preanal slightly enlarged; dorsal scale with feeble single keel, ventrals have a tubercule like strong keel; majority of the specimens with no banding on their body, some specimens with feeble banding on the posterior 2/3 of the body with number of bands around 35–52; head length 10.1–16.8 mm; head width 3.1–5.6 mm; head depth 3.4–5.3 mm; snout-vent length 525.0–809.0 mm; tail length 50.0–85.0 mm. Dorsum light brown anteriorly rest of the body creamy brown without any markings or bands till tail. Head brown dorsally, ventral light brown.

Microcephalophis cantoris (Günther, 1864)
(Fig. 9, Table 1)

Materials examined (n=11). INDIA: ZSI 8231 Sand head, West Bengal; ZSI 8623 Mumbai, Maharashtra coll. Cockburn; ZSI 14459 Puri, Odisha, coll. Dr J.L. Hendley; ZSI 12587 Sargar road, West Bengal, coll. S. Ebon. Esq.; ZSI 18334 St. 14 , Sandy Bay, North west of Nazarath point, Portuguese, coll. S.W. Kemp in August–September 1916; ZSI 22579 From fishermen net at Saminanpathi 5 miles North Portonvo, Madras, Tamil Nadu, Collector: Dr A. Danial on 12.05.1960; ZSI 23029 Gopalpur, Ganjam, Odisha, coll. D.P.Sanyal on 15.11.1971; ZSI 23149 Digha coast, Midnapore, West Bengal, coll. T.K.Sen (Indo-Japanese survey) on 27.03.1975; BNHS 2369 (2 ex) Madras, Tamil Nadu, coll. Maj. F. Wall on 31.12.1907; BNHS 2370 Karwar, Uttar Kannada, Karnataka, coll. C.C.Boyd on 31.12.1907.

Description and Variation. Head very small, elongate, body long slender anteriorly and thick compressed posteriorly; snout projecting beyond the lower jaw; rostral higher than broad, extending well on to the upper surface of the snout; prefrontal slightly elongated, touching the 3rd supralabial, in two specimens prefrontal in contact with both 2nd and 3rd supralabial (ZSI 22579 and ZSI 23149); frontal smaller than the distance from the rostral, in 3 specimens it is larger than the distance from the rostral (BNHS 2369 A, ZSI 14459 and ZSI 8623), in 2 specimens frontal is as long as the distance from the rostral (ZSI 8231 and ZSI 12587); parietal longer than broad; single anterior temporal; one supraocular on each side of head; one preocular on each side of head; one postocular on each side of head; 6 supralabial on each side of the

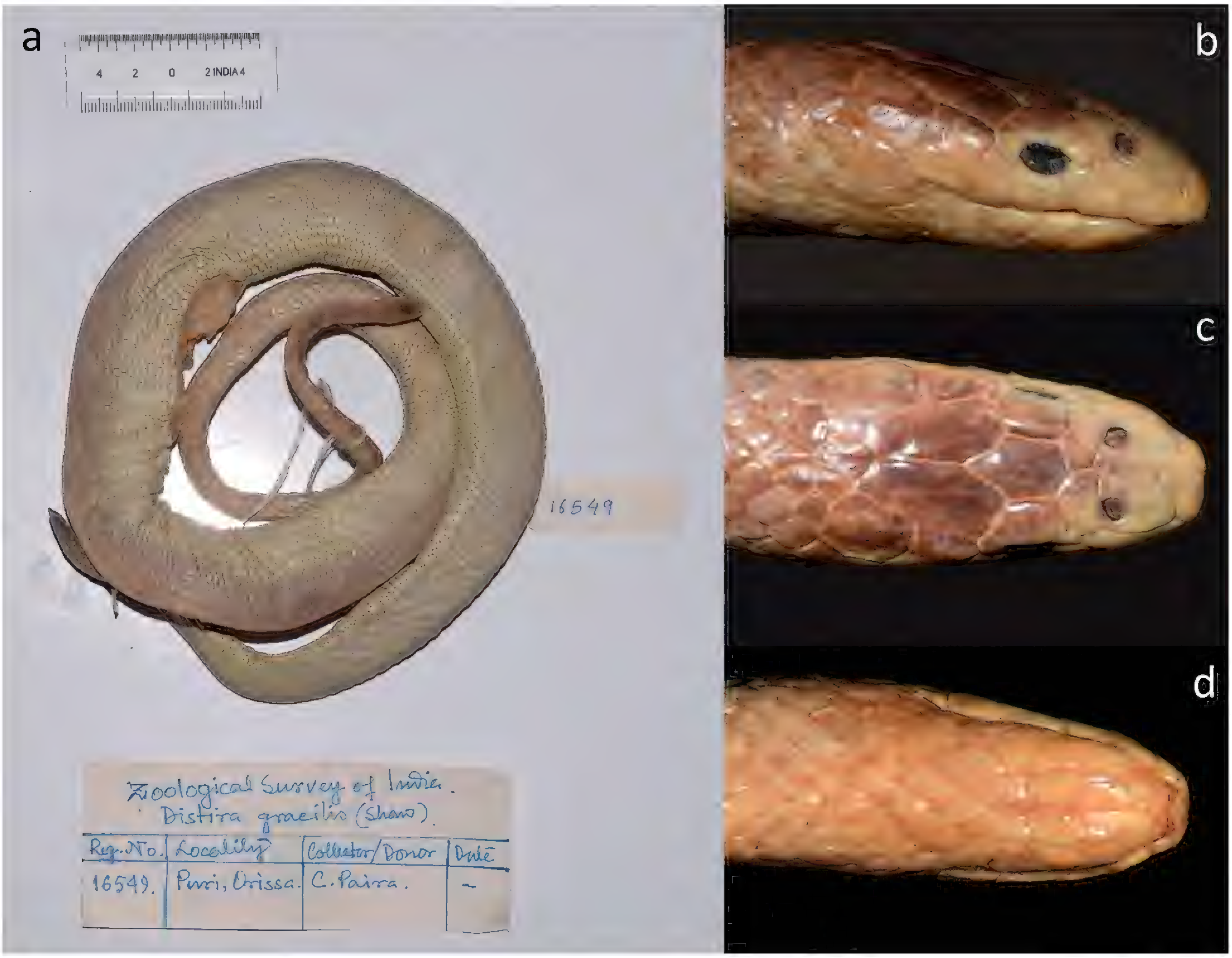
a
4 2 0 2 INDIA 4
16549
Zoological Survey of India.
Distira gracilis (Shaw)
Reg. No. | Locality | Collector/Donor | Date
16549. | Puri, Orissa. | C. Paira. | –
b
c
d

Fig. 8. *Microcephalophis gracilis* (ZSI 16549). **A**. Entire. **B**. Head lateral. **C**. Head dorsal. **D**. Head ventral profiles. Photo: S. Mondal.

head, 3rd and 4th touching the eye, 5th largest; 7–8 infralabials, 4 infralabials touching chin shields; chin shields well developed, anterior pair in contact with each other whereas posterior pair separated by a scale, anterior pair larger than the posterior pair; scales around neck 23–25; scales around midbody 30–37, scales at the thickest part of the body 40–43; ventrals 383–430, distinct from the adjacent dorsal scale anteriorly, median furrow divides the ventral into two posteriorly; preanal small, in 3 specimens it is slightly enlarged (ZSI 18334, BNHS 2369B and BNHS 2370); dorsal scale have single feeble keel, dorsal scales adjacent to the ventrals have 3–4 dot-like keels, ventrals have small keel; number of bands on the body 49–60, bands are closely placed extending towards ventrals, in one specimen dorsum is uniform brown colouration (ZSI 12587), in another specimen bands present anterior 1/3 have feeble 25 bands, number of bands on tail 2–8; head length 10.4–21.7 mm; head width 3.7–11.1 mm; head depth 3.1–10.2 mm; snout-vent length 495.0–1305.0 mm; tail length 55.0–120.0 mm. Dorsum moderately brown with feeble darker brown bands more prominent anterior part of the body than posterior half, ventral light creamy brown till tail. Head dark brown, lower labial light brown.

DISCUSSION

Some studies from India report on a few rare sea snake species. Murthy (1977) reported on sea snakes in Madras coast including rare species such as *H. jerdoni, H. viperinus* and *M. gracilis*. Talukdar & Dattagupta (1980) reported *H. mamillaris* and *M. gracilis* from Bengal coast. Murthy (1987) and Vekateswarlu et al. (1995) reported *H. obscurus* from Orissa Coast. Das & Chandra (1994) reported one species of rare sea snake, *M. cantoris* from Andaman and Nicobar Islands. In a study on the Gulf of Mannar coast near Palk Strait, Lobo (2006) reported rare species such as *H. viperinus, H. jerdoni* and *M. gracilis*. Karthikeyan & Balasubramanian (2007) reported *H. stricticollis, H. viperinus* and *M. gracilis* from Chennai-Pondicherry-Cuddalore-Nagapattinam coast.

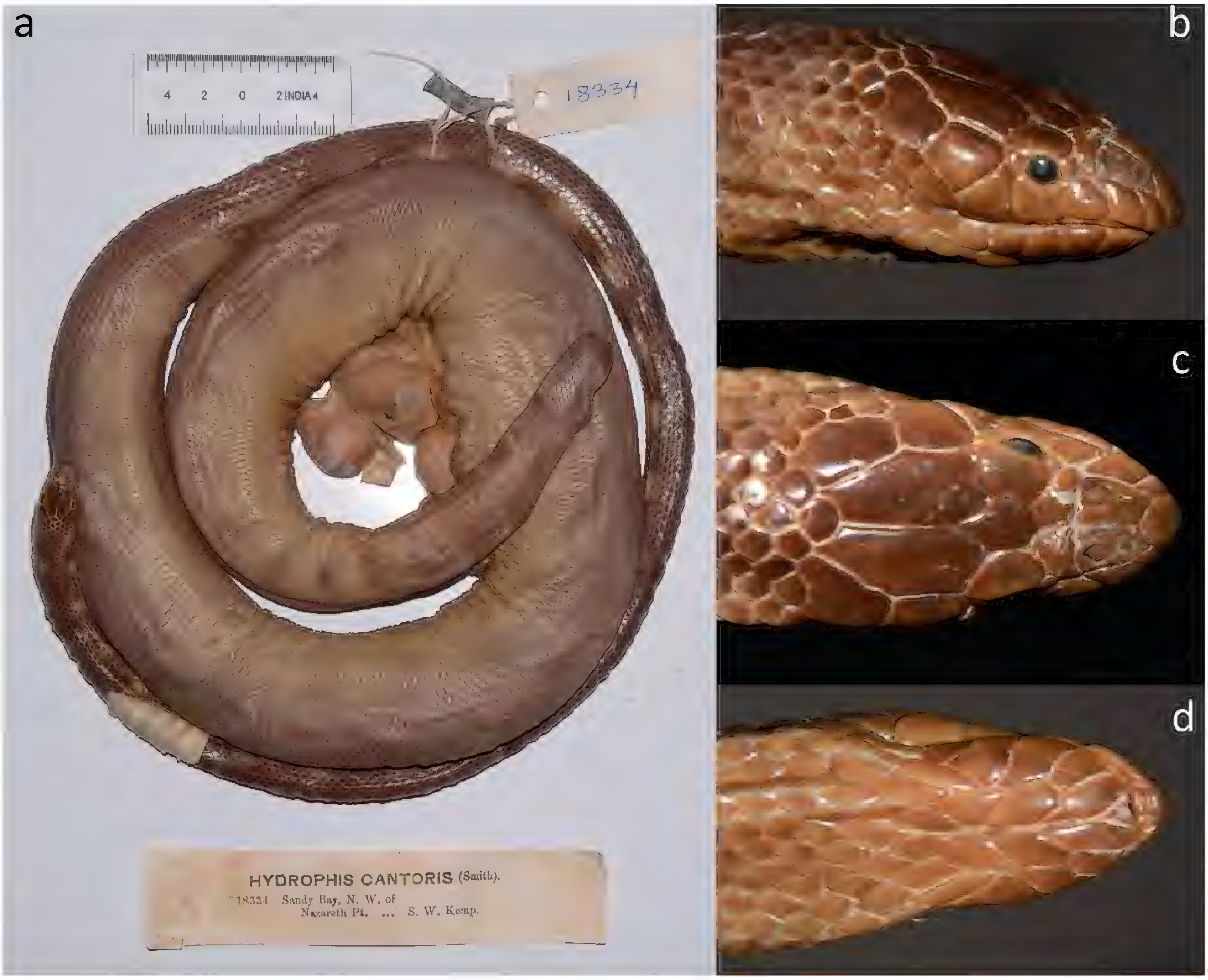
a
b
c
d
4 2 0 2 INDIA 4
18334
HYDROPHIS CANTORIS (Smith).
18334 Sandy Bay, N. W. of
Nazareth Pt. ... S. W. Kemp.

Fig. 9. *Microcephalophis cantoris* (ZSI 18334). **A**. Entire. **B**. Head lateral. **C**. Head dorsal. **D**. Head ventral profiles. Photo: S. Mondal

Kannan & Rajagopalan (2008) reported *H. jerdoni* off Mangalore coast, in the Arabian Sea. Damotharan et al. (2010) reported *M. gracilis* from Parangipettai coast. They also reported a sea krait *Laticauda colubrina* from Parangipettai, whereas previous literature states it to be absent in mainland coast (Smith, 1943). Similarly, Dabhi et al. (2019) reported *H. mamillaris* from Gujarat coast, but the substantiations sadly fall short of normal standards and it is treated doubtful at best. Put together, the above reports are the available works that recorded uncommon, rare or little-known species of sea snakes in any part of the Indian coastlines.

On the other hand, as previously stated, data on commoner species come in frequently and in large quantities. As an example, we wish to highlight the fact that Wall (1918) expressly stated his collectors in Madras coast not to bring in any more *H. schistosus* specimens, as it got far more numerous than necessary. For one rare species, *Hydrophis* (earlier *Astrotia) stokesi* (Gray, 1846), we could not locate even a single specimen in these museums. Whitaker & Captain (2004) dealt with that species with a picture depicting an extralimital population, i.e., from the Visayan sea, Philippines. Seen against that backdrop of Indian sea snake literature, this fresh set of descriptions of selected few rare species will facilitate their identification. It is hoped that this exercise of analyzing sea snake reports, identifying rarer sea snake species and specifically focusing on such rare species whilst giving this treatment on historical material, will help boost knowledge base on Indian populations of these rare sea snakes.

Acknowledgements. We thank our respective organisations for encouraging our research activities. At the Zoological Survey of India, we thank the Director, ZSI Kolkata, for her kind support all throughout. At the Kalinga Foundation, thanks are due to the Director and Trustees, for encouraging our joint research activities. SRG thanks Dr Sanjay Molur, Zoo Outreach Organi-

Table 1. Morphological characters (measures in mm) of voucher specimens of rare sea snakes (*Hydrophis, Microcephalophis*) housed at the ZSI Kolkata and BNHS collections.

characters	***Hydrophis jerdonii***	***Hydrophis lapemoides***	***Hydrophis mamillaris***	***Hydrophis nigrocinctus***	***Hydrophis stricticollis***	***Hydrophis viperinus***	***Hydrophis obscurus***	***Microcephalophis gracilis***	***Microcephalophis cantoris***
temporal	1	1 or 1+2	2+2	2+3	1 or 1+2	2	1	1	1
supraocular	1	1	1	1	1	1	1	1	1
preocular	1	1	1–2	1–2	1	1	1	1	1
postocular	1	2–3	1–2	2	1–2	1–2	1	1	1
supralabials (touch eye)	6 (3,4)	7–8 (3,4,5)	6–7 (3,4,5)	7 (4)	7 (3,4)	7–8 (3,4,5)	6–7 (3,4)	6 (3,4)	6 (3,4)
infralabials (touch chin shields)	6–7 (1–3)	8–9 (1–3)	7–8 (1–4)	7–8 (1–3)	9 (1–3)	7–9 (1–4)	6–8 (1–4)	7 (1–4)	7–8 (1–4)
anterior scalerows	16–18	29–31	25–30	27–30	32–39	28–33	19–23	19–20	23–25
midbody scalerows	19–22	39–41	33–45	36–42	44–46	41–48	26–32	27–38	30–37
ventrals	214–258	310–345	260–350	300–332	378–451	225–266	264–363	228–285	383–430
preanals	slightly enlarged	enlarged	small	slightly enlarged	small	slightly enlarged	small	slightly enlarged	small
head length	12.1–24.1	20.3–23.8	12.8–17.4	12.9–27.3	19.3	13.8–25.1	9.1–16.1	10.1–16.8	10.4–21.7
head width	4.9–10.7	7.0–12.0	5.4–7.1	4.3–12.3	7.6	7.2–12.5	3.1–6.7	3.1–5.6	3.7–11.1
head depth	4.0–7.6	8.3–8.7	4.2–6.8	4.0–8.8	7.3	4.6–9.3	2.5–6.4	3.4–5.3	3.1–10.2
snout to vent length	375–958	643–863	355–743	460–1105	890–955	260–679	395–1245	525–809	495–1305
tail length	50–110	68–88	35–80	53–135	90–130	38–83	43–140	50–85	55–120
body bands	30–43	37–50	40–55	54–56	44–46	Absent	45–69	35–52	49–60
tail bands	2–4	2–5	2–9	6–10	Absent	Absent	2–9	Absent	2–8

zation for extending logistic support. Thanks are due to Director, Dy. Director and O.D. Adhikari of the BNHS.

REFERENCES

Ahmed S (1975) Sea-snakes of the Indian ocean in the collections of the Zoological Survey of India together with remarks on the geographical distribution of all Indian ocean species. Journal of the Marine Biological Association of India 17 (1975): 73

Boulenger GA (1890) The fauna of British India, including Ceylon and Burma. Reptilia and Batrachia. Taylor and Francis, London

Boulenger GA (1896) Catalogue of the Snakes in the British Museum (Natural History). Vol. III, Containing the Colubridae (Opisthoglyphae and Proteroglyphae), Amblycephalidae and Viperidae. British Museum (Natural History), London

Chandrasekar K, Balakrishnan S, Arun G, Satyanarayana C, Venkataraman K (2018) New Observation of Intertwined Annulated Sea Snake *Hydrophis cyanocinctus* (Reptilia: Elaphidae: Hydrophiinae) from Pirotan Island, Gulf of Kachchh. Indian Journal of Geo Marine Sciences 47 (12): 2465–2468

Costello MJ, Basher Z, McLeod L, Asaad I, Claus S, Vandepitte L, Bates AE, Yasuhara M, Gislason H, Edwards M, Appeltans W, Enevoldsen H (2017) Methods for the study of marine biodiversity. Pp. 29–163 in: The GEO handbook on biodiversity observation networks. Springer, Cham

Costello MJ, Coll M, Danovaro R, Halpin P, Ojaveer H, Miloslavich P (2010) A census of marine biodiversity knowledge, resources, and future challenges. PloS one 5 (8): e12110

Dabhi J, Poriya P, Gadhvi I (2019) Diversity of sea snakes along the Saurashtra coast, Gujarat, India. Life sciences leaflets 108: 8–10

Damotharan P, Arumugam M, Vijayalakshmi S, Balasubramanian T (2010) Diversity, biology, and ecology of sea snakes (Hydrophiidae) distributed along the Parangipettai Coast, southeast coast of India. International Journal of Current Research 4: 62–69

Daniel JC (2002) The book of Indian reptiles and amphibians. Bombay Natural History Society, Oxford Publishers, Mumbai

Das I, Chandra K (1994) Two snakes new to Andaman and Nicobar Islands. Journal of Andaman Science Association 10 (1&2): 114–115

Das I, Chaturvedi N (1998) Catalogue of herpetological types in the collection of the Bombay Natural History Society. Hamadryad 23: 150–156

Das I, Gayen NC (2004) Addenda and corrigenda to the catalogue of reptile types in the collection of the Zoological Survey of India. Hamadryad 28: 95–97

Das I, Dattagupta B, Gayen NC (1998) History and catalogue of reptile types in the collection of the Zoological Survey of India. Journal of South Asian Natural History 3 (2): 121–172

Das I (2002) A photographic guide to snakes and other reptiles of India. New Holland Publishers, London

Dowling HG (1951) A proposed standard system of counting ventrals in snakes. British Journal of Herpetology 1: 97–99

Dsouza S, Rao C (2021) Demographics and reproductive biology of *Hydrophis schistosus* may make it more resilient to bycatch effects than other sea snakes. Regional Studies in Marine Science 47: 101948

Ganesh SR, Asokan JR (2010) Catalogue of Indian herpetological specimens in the collection of the Government Museum Chennai, India. Hamadryad 35 (1): 46–63

Ganesh SR, Bhupathy S, Karthik P, Rao B, Babu S (2020) Catalogue of herpetological specimens from peninsular India at the Sálim Ali Centre for Ornithology & Natural History (SACON), India. Journal of Threatened Taxa 12 (9): 16123–16135

Ganesh SR, Nandhini T, Samuel VD, Sreeraj CR, Abhilash KR, Purvaja R, Ramesh R (2019) Marine snakes of Indian coasts: historical resume, systematic checklist, toxinology, status, and identification key. Journal of Threatened Taxa 11 (1): 13132–13150

Günther ACLG (1864) The Reptiles of British India. Ray Society, London. https://doi.org/10.5962/bhl.title.5012

Jeyabaskaran R, Lavanya S, Bose J, Vysakhan P, John S, Prema D, Kripa V (2015) Report on occurrence of Yellow Sea Snake Hydrophis spiralis off Kerala coast. Marine Fisheries Information Service; Technical and Extension Series (226): 13–14

Kalaiarasan V, Kanakasabai R (1994) Seasonal availability of sea snakes (Family: Hydrophidae) in the Madras waters. Cobra 16: 18–19

Kannan P, Rajagopalan M (2008) Distribution of Sea Snakes in the Indian Coastal Waters. Scientific Transactions in Environment and Technovation 1 (4): 218–223

Karthikeyan R, Balasubramanian T (2008) Feeding and reproductive behavior of captive sea snakes *Hydrophis cyanocinctus*. Applied Herpetology 5 (1): 75

Karthikeyan R, Vijayalakshmi S, Balasubramanian T (2008) Feeding and parturition of female annulated sea snake *Hydrophis cyanocinctus* in captivity. Current Science: 660–664

Kumar AB, Kumar MS, Deepthi GR, Mithun S (2007) Sea snakes associated with trawl by-catch of Kerala Coast, India. Cobra 1 (1): 1–4

Lobo AS (2006) Sea snakes of the Gulf of Mannar Marine National Park. The species and their conservation. A Report Submitted to The Rufford Fundation, UK

Lobo AS, Vasudevan K, Pandav B (2005) Trophic ecology of *Lapemis curtus* (Hydrophiinae) along the western coast of India. Copeia 2005 (3): 637–641

Lobo A, Pandav B, Vasudevan K (2004) Weight-length relationships in two species of marine snakes along the coast of Goa, Western India. Hamadryad 29: 89–93

Mondal S, Ganesh SR, Sethy PGS, Raghunathan C, Raha S, Sarkar S (2022) Redescriptions of the type specimens of synonymous nominal taxa of sea snakes (Serpentes: Elapidae: *Hydrophis, Laticauda*) at the Zoological Survey of India. Zootaxa 5169 (4): 301–321

Murthy TSN, Rama Rao KV (1988) Snakes of the Chilka Lake, Orissa, India. The Snake 20: 67–73

Murthy TSN (1977) On sea snakes occurring in Madras waters. Journal of the Marine Biological Association of India 19 (3): 68–72

Murthy TSN & Rama Rao KV (1976) Studies on the sea snakes of the Madras coast in captivity. Newsletter of the Zoological Survey of India 2 (4): 124–125

Murthy TSN (1987) Herpetofauna of the Chilka Lagoon, Orissa, India. British Herpetological Society Bulletin 21–22: 8–12

Muthukumaran M, Rao AVB, Alexandar R (2015) Threats of passive fishing activities on sea snake *Enhydrina schistosa* (Daudin 1803) of Puducherry coast, India. International Journal of Pure and Applied Zoology 3 (1): 53–58

Myers GS (1947) Murray’s Reptiles of Sind, with a Note on Three Forgotten Descriptions of Indian Sea-Snakes, Published Therein. Herpetologica 3 (5): 167–168

Padate VP, Baragi LV, Rivonker CU (2009) Biological aspects of sea snakes caught incidentally by commercial trawlers off Goa, west coast of India. Journal of Threatened Taxa 12 (1): 606–612

Palot MJ, Radhakrishnan C (2010) First record of yellow-bellied sea snake *Pelamis platurus* (Linnaeus, 1766) (Reptilia: Hydrophiidae) from a riverine tract in northern Kerala, India. Journal of Threatened Taxa 2 (9): 1175–1176

Parmar DS (2018) First record of a Yellow-bellied SeaSnake, *Hydrophis platurus* (Linnaeus 1766), from Gujarat, India. Reptiles & Amphibians 25 (2): 137–138

Parmar, DS (2019a). First record of an Annulated Seasnake, *Hydrophis cyanocinctus* (Daudin 1803), from the Surat District, South Gujarat, India. Reptiles & Amphibians 26 (1): 56–57

Parmar DS (2019b) A Dwarf Seasnake, *Hydrophis caerulescens* (Shaw 1802), Dog-faced Water snake, *Cerberus rynchops* (Schneider 1799), and Little File snake, *Acrochordus granulatus* (Schneider 1799) from the Surat District, Gujarat, India. Reptiles & Amphibians 26 (2): 134–139

Phipson HM (1888) Catalogue of snakes in the society‘s collection. Journal of the Bombay Natural History Society 3 (1): 49–53

Prachi H, Ramesh C (2016) A comprehensive report on the Hook-nosed Sea Snake *Enhydrina schistosa* (Daudin, 1803). Newsletter of the South Asian Reptile Network 18: 19

Rao C, Dsouza S, Gupta T, Manoharakrishnan M, Lobo AS (2021) Fisheries induced shift in sea snake community assemblages along the Konkan coast, India. Aquatic Conservation: Marine and Freshwater Ecosystems 31 (9): 2402–2411

Sclater WL (1891) List of Snakes in the Indian Museum. Printed by the order of the Trustees of the Indian Museum, Calcutta

Smith MA (1926) Monograph on the Sea Snakes. (Hydrophiidae). British Museum, London

Smith MA (1943) The Fauna of British India, Ceylon and Burma, Including the Whole of the Indo-Chinese Sub-Region. Reptilia and Amphibia. Vol. 3 (Serpentes). Taylor and Francis, London

Talukdar SK, Dattagupta B (1980) Notes on the occurrence of the sea snakes, *Hydrophis mamillaris* (Daudin) and *Microcephalophis gracilis* (Shaw) from West Bengal. Journal of the Marine Biological Association of India 18 (2): 389–391

Tambre G, Mote S, De K, Yogi D, Jadhav M, Ingole B...., Nanajkar M (2020) By-catch mortality of beaked Sea Snake *Hydrophis schistosus* (Daudin, 1803) by entanglement in shore-seine operation in Goa-India. Acta Biologica 27: 67–76

Theobald W (1868) Catalogue of Reptiles in the Museum of the Asiatic Society of Bengal (Vol. 32). Printed at the Baptist Mission Press, Bengal

Theobald W (1876) Descriptive catalogue of the reptiles of British India. Thacker, Spink & Co., Calcutta.

Tripathy B (2006) Observations on Hook-nosed Sea snake, *Enhydrina schistosa* (Daudin) and Black and Yellow Sea Snake, *Pelamis platurus* (Linnaeus) at Rishikulya, Orissa, India. Cobra 63: 4–6

Venkateswarlu T, Pattanayak JG, Nahar SC, Mohapatra A (1995) On the collection of snakes from Mahanadi Estuary (Orissa, India). The Snake 27 (1): 49–52

Venkatraman C, Padmanaban P, Sivaperuman C (eds) (2015) Seasonal Abundance of Sea Snakes on the Chennai Coast, Southern India. Pp. 249–259 in: Marine Faunal Diversity in India. Academic Press. https://doi.org/10.1016/B978-0-12-801948-1.00016-1

Wall F (1906) A descriptive list of the sea snakes (Hydrophiinae) in the Indian Museum, Calcutta. Memoirs of the Asiatic Society of Bengal 1 (14): 277–299

Wall F (1909) A monograph of the sea snakes (Hydrophiinae). Memoirs of the Asiatic Society of Bengal 2 (8): 169–251

Wall F (1918) Notes on a collection of sea snakes from Madras. Journal of the Bombay Natural History Society 21: 599–607

Whitaker R, Captain A (2004) Snakes of India—the field guide. Draco books, Chengelpet, Tamil Nadu

Bonn zoological Bulletin 72 (2): 223–233
2023 · Schmied H. et al.
https://doi.org/10.20363/BZB-2023.72.2.223

ISSN 2190–7307
http://www.zoologicalbulletin.de

Research article

urn:lsid:zoobank.org:pub:B1045D56-14E5-48BD-B8CE-81C6AD15D215

Functional morphology of water holding by feathers of sandgrouse (Aves: Pteroclidae): first evidence for directed hydroscopic motion in animals

Heiko Schmied[1,*], David Klocke[2] & Alexander Rüttgers[3]

[1] *Institute of Crop Science and Resource Conservation, Agroecology and Organic Farming Group, University Bonn, Auf dem Hügel 6, D-53121 Bonn, Germany*
[2] *Institute of Zoology, University of Bonn, Poppelsdorfer Schloss, Meckenheimer Allee 169, D-53115 Bonn, Germany*
[3] *Institute for Software Technology, High-Performance Computing Department, German Aerospace Center (DLR)*
** Corresponding author: Email: schmied@uni-bonn.de*

[1] urn:lsid:zoobank.org:author:23854168-99EA-4DE5-A56A-CAF810D3C26B
[2] urn:lsid:zoobank.org:author:CF4F1E74-7E31-45A4-A6A4-C461136A03DB
[3] urn:lsid:zoobank.org:author:F84A3DD1-A646-46F8-8A70-4E6A92E7590D

Abstract. The water transport of sandgrouse (Pteroclidae) presents one of the most amazing behaviors in birds. The unique ability to absorb water by their abdominal feathers was disclaimed over decades but is described here for the first time. For a comprehensive picture of the morphological and physical parameters, we used different approaches in pterylography, functional morphology, biomechanics, new measurement techniques and calculations of wetting properties, absorption capacity tests and numerical simulations. We show that the ability of carrying large amounts of water is caused by different factors like: the distribution of feathers on the underside, a specialized feather margin, a well-directed hygroscopic alteration of the microstructure, which is the first discovered in the animal kingdom and a unique hydrophilicity of the feather material. Determination of absorption capacities of feathers in sandgrouse and non-sandgrouse species clearly shows the effects of the different adaptations in feather structure. Numerical simulations determine the adhesive force of the feather microstructure of sandgrouse and show that minimal changes of the structure lead to a complete loss of the specialized properties. From this we conclude that the microstructure of sandgrouse feathers has evolved to absorb the largest possible volume of water with as little material as possible. Our results show that the water transport in sandgrouse is based on the interaction of many highly derived characteristics.

Key words. Sandgrouse, *Pterocles*, biomechanics; contact angle; wettability; hygroscopic motion.

INTRODUCTION

Sandgrouse (Pteroclidae) mostly live in arid areas and feed nearly exclusively on dry seeds so in consequence they need to drink daily (MacLean 1983; de Juana 1997; Lloyd et al. 2000). Because sources of surface water are up to 80 kilometers away from the nesting sites (MacLean 1968), the young depend on their parents for drinking (de Juana 1997). Therefore, the males of all sandgrouse species, except of the Tibetan Sandgrouse (*Syrrhaptes tibetanus*), absorb water with their abdominal feathers (on average 25 ml for males, less for females; Cade & MacLean 1967) and fly to their young that drink out of the parents' plumage (Cade & MacLean 1967; MacLean 1983; de Juana 1997). This behavior was disowned as a myth by ornithologists over decades in the twentieth century until Cade & MacLean (1967) firstly documented this behavior in the wild. The so-called belly-soaking of the Charadriidae is similar to the water transport of sandgrouse. If temperatures are very high at their breeding sites, adult birds wet their belly feathers and then sit on the clutch or nestlings (MacLean 1975). The behavior was interpreted as cooling the eggs, the nestlings and/or the breeding adult bird (Maclean 1975, Seymour & Ackerman 1980, Amat & Masero 2007, 2009). Sporadically this behavior also occurs in other bird families, e.g., in the Sternidae (Grant 1981), Rhynchopidae (Strong & Miyako 2004), Recurvirostridae (Goutner 1984) and Hirundinidae (Jackson & Schardien 1981). Belly-soaking often only occurs during particularly hot periods (Begg & Maclean 1976). However, it has never been described that young birds ingested water. In addition, the feather structures of plover species do not show any characteristics that indicate specialization for water absorption (own data, unpublished). In sandgrouse the feather microstructure of specialized abdominal feathers changes by wetting. Rijke (1972) and Joubert & MacLean (1973) tried to explain this process by a molecular change of keratin but could not give a biomechanical explanation for the microstructural movement. Therefore, the explanation for the extraordinary wetting properties and the physical basis for the efficiency of water transport are still unknown.

Received: 26.05.2021
Accepted: 24.11.2023

Corresponding editor: T. Töpfer
Published: 28.11.2023

We used different kinds of morphological, physical and numerical approaches to explore the water transport of sandgrouse. The pterylography of sandgrouses and some species of pigeons (Columbidae), their close relatives, was studied to clarify whether the distribution and orientation of the feathers is already specialized in water transport, which was not considered by former studies. We investigated the feather morphology of nine sandgrouse and four none-sandgrouse species macro- and microscopically. This enabled us to compare variations in feather structure within the Pteroclidae (including *S. tibetanus*) and to demonstrate differences to closely related land birds (Pigeons, sister taxon of the Pteroclimesites [Sandgrouse & Mesites]; Sangster et al. 2022), unrelated land birds (Finches, Fringillidae) as well as bird taxa which always get in contact with water (Grebes, Podicepididae and Cormorants, Phalacrocoracidae). To describe the mechanism of water transport we examined the change in the internal structures of the feathers when they were wetted.

The internal composition of the barbules was investigated by semi-thin sections, freeze fractures and scanning electron microscope (SEM) to understand the microstructural movements. Furthermore, the biomechanical properties of different parts of the feather material were directly measured by atomic force microscopy under dry and wet conditions. The wetting properties of feathers were described by direct measurements of the material contact angle in sandgrouse and non-sandgrouse species. Calculations of the intrinsic contact angle were made (according to Cassie & Baxter 1944; Wenzel 1936) to explain the different wetting properties adapted to the birds' mode of life. We measured the different water absorption capacities of complete and experimentally modified sandgrouse feathers as well as feathers from non-sandgrouse species according to Thomas & Robin (1977). This enabled us to compare the morphology and wetting properties with water intake and to test the hypothesis that water absorption of sandgrouse feathers follows the Michaelis-Menten saturation curve. To understand the intensity of the adhesive forces inside the sandgrouse microstructure when wetted, we generated numerical simulations with an original and a varied morphology and observed their ability to retain water droplets against gravity. For terminology of feather microstructure we refer to Sick (1937) and Dove (1997).

MATERIALS AND METHODS

(a) Pterylography

Feathers were plucked on the ventral side of one dead specimens of Namaqua Sandgrouse (*Pterocles namaqua*), of several partial skins of Double-banded Sandgrouse (*P. bicinctus*) and of one Common Wood Pigeon (*Columba palumbus*) from the Zoological Collection of the Department Animal Ecology (University of Bonn). The number of breast and belly feathers and their orientation were recorded. Distributions of feather tracts (pterylae) were drawn.

(b) Feather morphology

Several breast feathers of males (in some species also of females) of nine sandgrouse species (*P. namaqua, P. bicinctus, P. burchelli, P. exustus, P. guttularis, P. orientalis, P. quadricinctus, P. lichtensteinii, Syrrhaptes tibetanus*) and other non-sandgrouse species [Common Wood Pigeon, Cormorant (*Phalacrocorax carbo*), Grosbeak (*Coccothraustes coccothraustes*), Little Grebe (*Tachybaptus ruficollis*)] were photographed (Nikon D40x) and examined regarding their microstructure by stereomicroscope (Zeiss Discovery V12 SteREO with AxioCam Icc 3).

Several breast feathers of *P. namaqua*, *P. bicinctus* as well as of Common Wood Pigeon, Cormorant, Grosbeak and Little Grebe were scanned using a scanning electron microscope (Hitachi S-2460N) at the Zoological Research Museum Alexander Koenig (Bonn). Measurements of the microstructures were made using ImageJ ver. 1.42.

Feather samples of *P. exustus, P. guttularis, P. orientalis, P. quadricinctus, P. lichtensteinii* originated from the Bavarian State Collection of Zoology (Munich); *P. burchelli, Syrrhaptes tibetanus* from the Zoological Research Museum Alexander Koenig (Bonn); *C. coccothraustes* from the Institute of Zoology (Bonn); *T. ruficollis* from the Dresden Zoo and *Phalacrocorax carbo* from the Department Animal Ecology (see above).

(c) Changes in feather configuration by wetting and structure of the barbules

Several breast feathers of *P. namaqua*, *P. bicinctus* and comparison species (see above) were submerged in distilled water and examined dry and wet by stereomicroscopy.

Semi-thin sections of sandgrouse barbules (*P. namaqua*, *P. bicinctus*) were made by microtome cuts (Microm HM 360) after embedding in synthetic resin (Epon® 812-Ersatzprodukt). The sections were stained with methylene blue azure or toluidine blue fuchsine and were examined for their internal structure under microscope (Zeiss Axioskop with AxioCam MRc).

For the freeze fracture process, wet breast feathers of *P. namaqua* were dipped into liquid nitrogen, crushed by a mortar and additionally well dried. Fractions at the basal part of the barbules were investigated by SEM (see above).

Serval ultrasonic cleaned *P. namaqua* feathers were embedded in synthetic resin (Epoxydharz L, R&G Faserverbundwerkstoffe GmbH) and cut by microtome (Reichert OmU3 with a diamond knife) at an angle of 90° to the longitudinal axis of the barbules. The cross-section surfaces of barbules were scanned by an atomic force microscope (Dimension 3100, Digital Instruments) under dry and wet conditions at the Institute of Zoology (Bonn) according to Klocke & Schmitz (2012).

(d) Wetting properties

For the measurement of the material contact angle θ, 6–8mm long tips of untreated apical barbs of *P. bicinctus, Phalacrocorax carbo* and *C. coccothraustes* were used. Additional samples of *C. coccothraustes* were dipped in acetone for a minute. Measurements of θ were made by a tensiometer (DCAT 21, DataPhysics Instruments GmbH) at the Institute of Textile Technology and Process Engineering (Denkendorf). Statistical analyses were made with OpenOffice Calc ver. 3.3.

For the calculating of the intrinsic contact angle θ*, measurements of the feather vane microstructure of *P. bicinctus, Phalacrocorax carbo*, *C. coccothraustes,* Bullfinch (*Pyrrhula pyrrhula*), Common Swift *(Apus apus)*, Cockatiel (*Nymphicus hollandicus*) were made by stereo microscope (see above) and ImageJ ver. 1.42. For measuring lengths on microstructure [2r = diameter of barbs; 2d = distance between barbs, according to Rijke (1970); h = height of barbs (only in *P. bicinctus*)] see Fig. 1B. The formula established by Rijke (1970) [(r+d)/r] for the estimation of structural wetting properties of bird feathers was calculated for every taxon based on average measurements of several feathers per species. Surface roughness (r` = proportion of real surface in contrast to geometrical projected surface) was calculated for *P. bicinctus* (without barbules) based on the specified measuring distances (see above). Calculations for the actual contact angle on feathers with heterogeneous wetting (Fig. 1A; *Phalacrocorax carbo*, *C. coccothraustes*, *Pyrrhula pyrrhula*, *Apus apus*, *Nymphicus hollandicus*) were made by the formulas (*a–c*) of Cassie & Baxter (1944):

a) $\cos\theta^* = f_s \cos\theta - f_a$
b) $f_s = ((\pi r/(r+d)) (1-\theta^*/180°)$
c) $f_a = 1 - r \sin\theta /(r+d)$

Calculations of θ* for feathers with homogeneous wetting (Fig. 1B; *P. bicinctus*) were made by the formula (*c*) of Wenzel (1936):

c) $\cos\theta^* = r' \cos\theta$

Feather samples of *Pyrrhula pyrrhula*, *Apus apus* and *Nymphicus hollandicus* originated from the Institute of Zoology (Bonn).

(e) Water absorption capacity

Breast feathers of *P. namaqua* (natural), *P. namaqua* (with the feather margin removed), *P. bicinctus*, Common Chaffinch (*Fringilla coelebs*), Domestic Canary (*Serinus serinus* forma *domestica*), House Sparrow (*Passer domesticus*), Yellowhammer (*Emberiza citrinella*), *Pyrrhula pyrrhula*, *C. coccothraustes*, Great Spotted Woodpecker (*Dendrocopos major*) and *Nymphicus hollandicus* were used for the determination of absorption capacity over time (15 s, 30 s, 60 s, 120 s and 240 s in distilled water) according to Thomas & Robin (1977). In contrast to Thomas & Robin (1977) the feathers were replaced on the water surface with the ventral side to get a more uniform wetting because of different curvature of the feathers. For weighing a micro scale (KERN AEJ 220-4M) was used. Statistical analyses were made by OpenOffice Calc ver. 3.3.

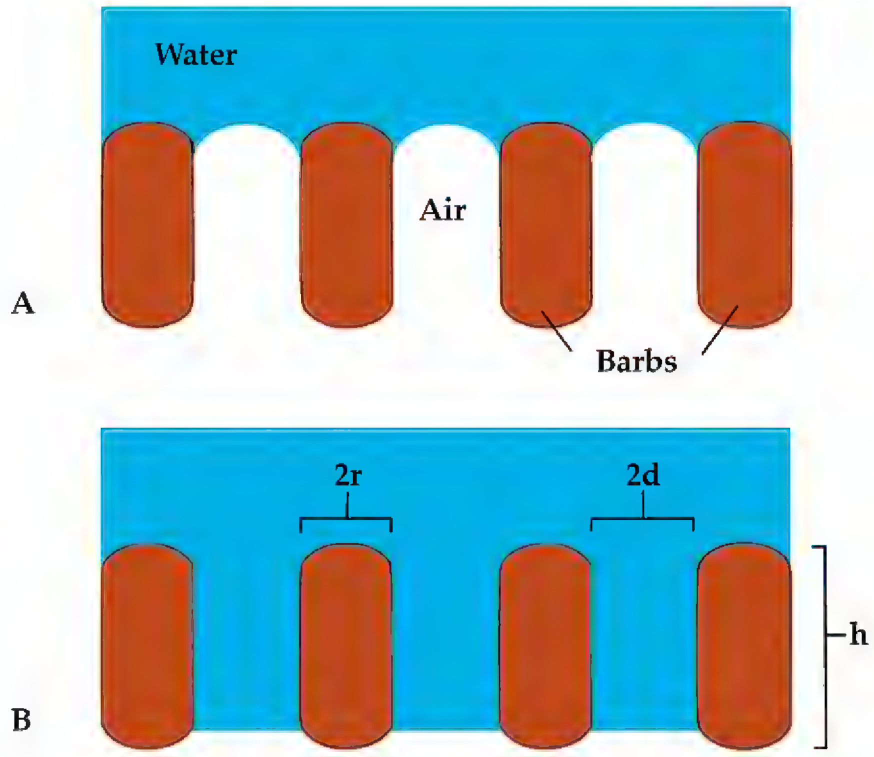

Fig. 1. Schematic cross section of wetted feather barbs (without barbules) with different wetting properties. **A**. Heterogeneous wetting with air pillows between the barbs (according to Cassie & Baxter 1944). **B**. Homogeneous wetting (according to Wenzel 1936). Measurements of microstructures (2r, 2d, h) are indicated.

Feather samples of *Fringilla coelebs*, *Serinus serinus* forma *domestica, Passer domesticus* and *Dendrocopus major* originated from the Institute of Zoology (Bonn). Samples of *Emberiza citrinella* originated from the Department Animal Ecology (Bonn).

(f) Numerical simulation

For modelling the adhesive forces in the sandgrouse's breast feathers, we built a computer model of the microstructure geometry (barbs and barbules in wet orientation, Fig. 2A–C) on the basis of the morphological description (see below). Then a falling water drop (volume: 0.034 mm^3; initial velocity of fall: 0.5 m/s; note that this initial velocity is below the terminal velocity of a water droplet with the same volume) was inserted for a three-dimensional flow simulation (Fig. 2E). Furthermore a modified geometry with 30% less barbules was created and tested in the same way (Fig. 2D). For performing the simulation, we used the two-phase flow solver NaSt3DGPF (Croce et al. 2010). For the discretisation of the Navier-Stokes equations, NaSt3DGPF employs a high-order

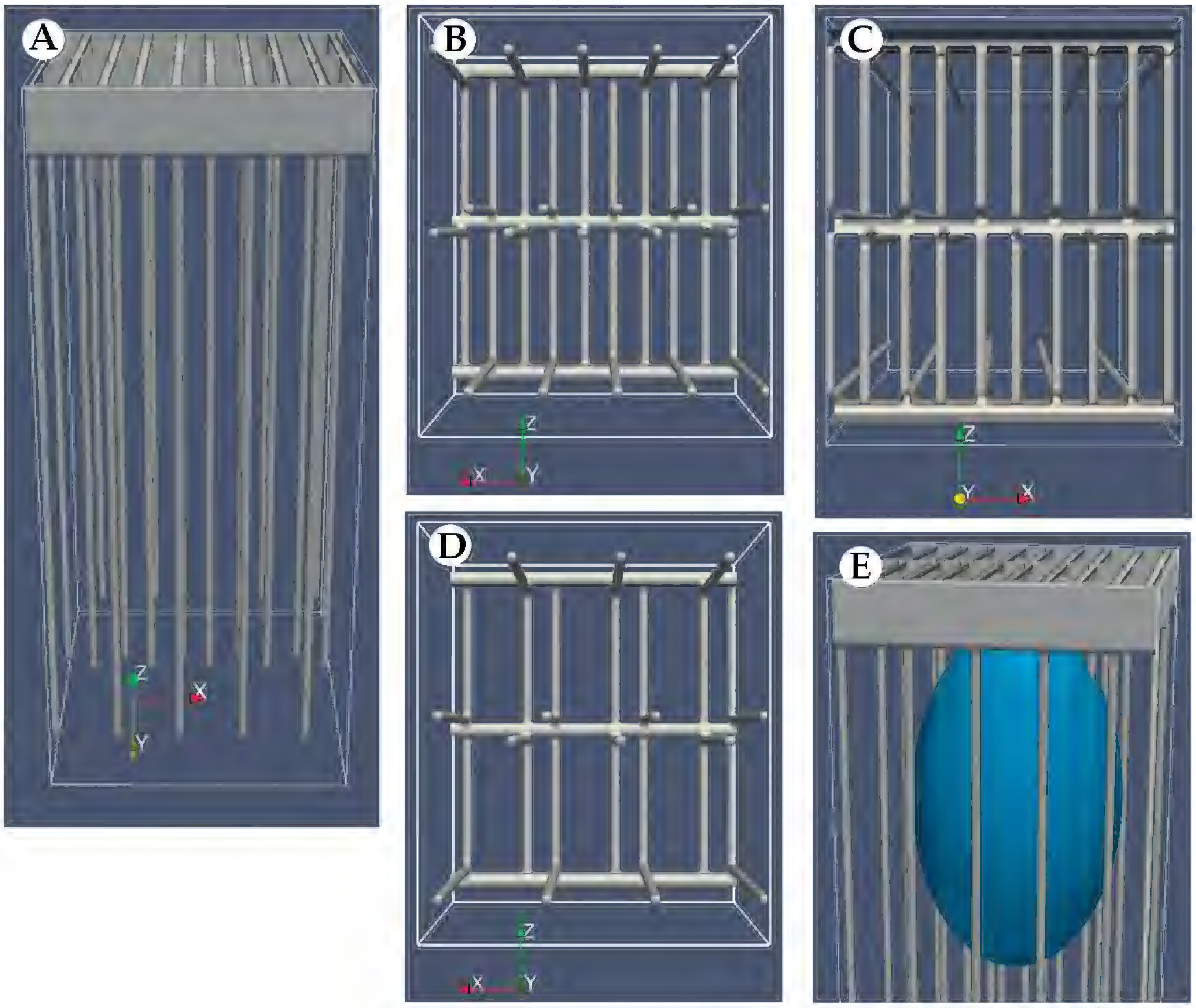

Fig. 2. Simulation space (0.5 × 1.2 × 0.6 mm) with inserted geometries. **A–C**. Sandgrouse microstructure geometry. **A**. Lateral view. **B**. Ventral view. **C**. Dorsal view. **D**. Ventral view on the varied geometry contains 30% less barbules. **E**. Initial conditions of the three-dimensional flow simulation with inserted water droplet inside the sandgrouse's microstructure geometry (lateral field of view).

finite difference method on a staggered grid in space and a third-order Runge-Kutta method in time. The two fluid phases are distinguished with the levelset technique and surface tension is modeled with the Continuum Surface Force (CSF) method. The flow solver is parallelized with MPI and with Nvidia's CUDA architecture to reduce computing time. The visualization was performed by ParaView ver. 3.1.4. We analyzed qualitative data such of droplet's barycenter position, its initial velocity and gave a measurement for the droplets' deformation in the two specified geometries over time.

RESULTS

(a) Pterylography

The pterylography of *P. namaqua* and *P. bicinctus* differs from that of *Columba palumbus* in the distribution and in the form of feather tracts (Fig. 3A–B). On the ventral side, about 1100 feathers were counted in sandgrouse (16 cm head-torso length) and about 830 in *C. palumbus* (22.8cm head-torso length). About 380 of the sandgrouse's feathers exhibit specialized characteristis for water transport. They are localized around the featherless area in the middle of the breast and belly (Fig. 3A). Specialized feathers of sandgrouse are oriented in clearly demarcated rows towards the featherless region whereas pigeon feathers are relatively evenly distributed and usually oriented caudally.

(b) Feather morphology

The breast feathers of sandgrouse (e.g., *P. namaqua*; Fig. 3C–D) differed from other body feathers by an elongated shape and by a distinct outer rim (unconnected distal ends of the barbs). In *S. tibetanus* (Fig. 3E) the breast feathers exhibit a reduced pennaceous vane and a large indistinct outer rim. Back feathers from *P. namaqua* (Fig. 3F) and other sandgrouse-species show a broad uniform vane and plumulaceous basis. Breast feathers of non-sandgrouse species show a large range of different morphologies (Fig. 4). Feathers of *C. palumbus* exhibit a large plumulaceous part and a relatively small pennaceous vane whereby in many cases the pennaceous region is completely lost. In *C. coccothraustes* feathers a large

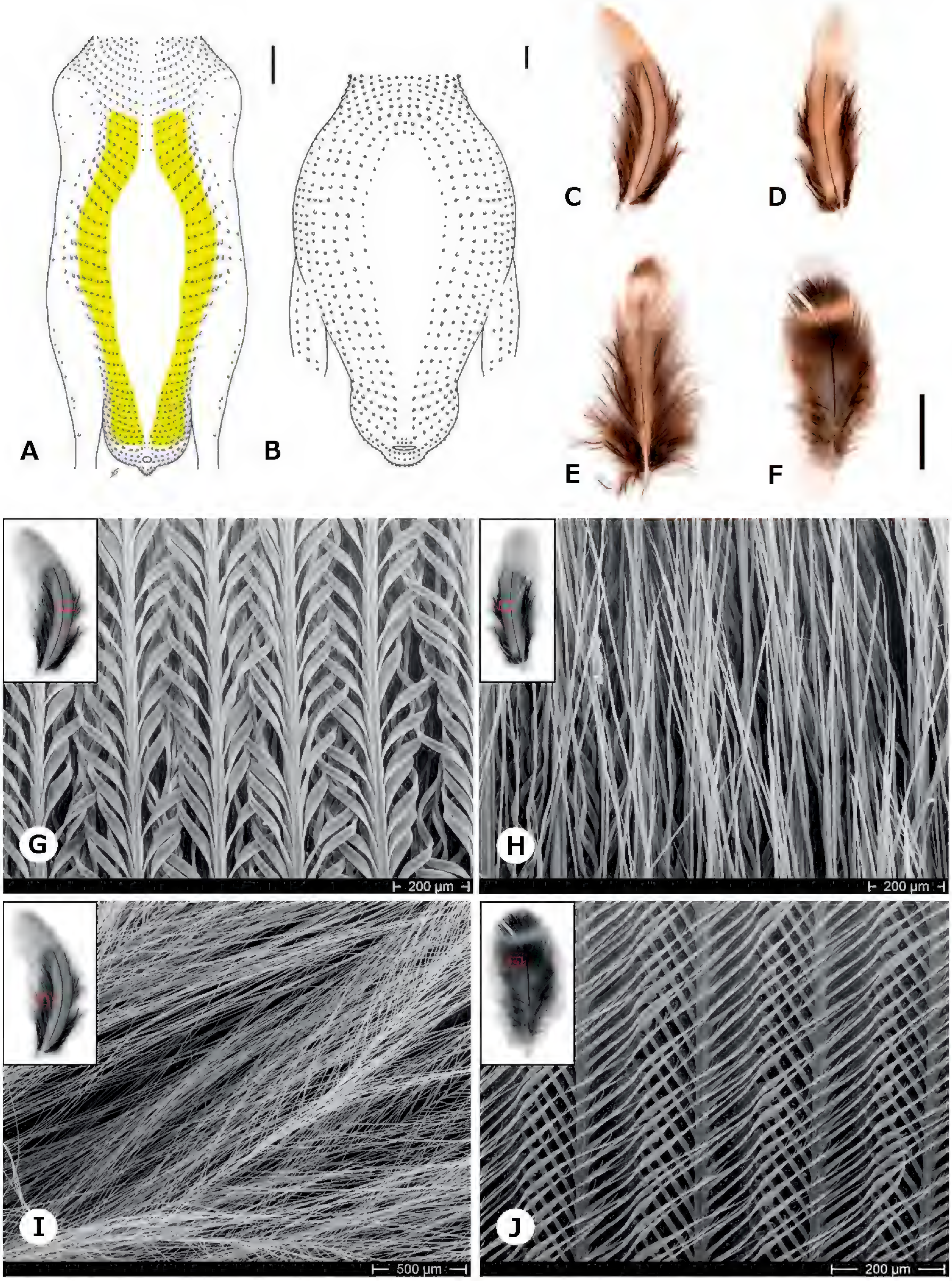

Fig. 3. **A**. Schematic pterylography of the breast and belly region of *P. namaqua* by means of follicle distributions. **B**. Schematic pterylography of the breast and belly region of *C. palumbus* by means of follicle distributions. **A–B**. Regions with follicles of specialized feathers for water transport are marked in yellow. **C–F**. Different body feathers of sandgrouse. **C**. Elongated breast feather of *P. namaqua*, dorsal view, with distinct outer rim. **D**. Elongated breast feather of *P. namaqua*, ventral view, with distinct outer rim. **E**. Dorsal view on breast feather of *S. tibetanus* with reduced pennaceous vane and indistinct outer rim. **F**. Back feather of *P. namaqua* with a uniform pennaceous vane and plumulaceous basis. **G–J**. SEM pictures of *P. namaqua* feather microstructure. **G**. Breast feather vane, dorsal view. **H**. Breast feather vane, ventral view. **I**. Loose barbs and elongated barbules of the outer rim of a breast feather, dorsal view. **J**. Microstructure of barbs and barbules (with and without barbicels) of a back feather vane, dorsal side. Scale bars: A–F = 1cm.

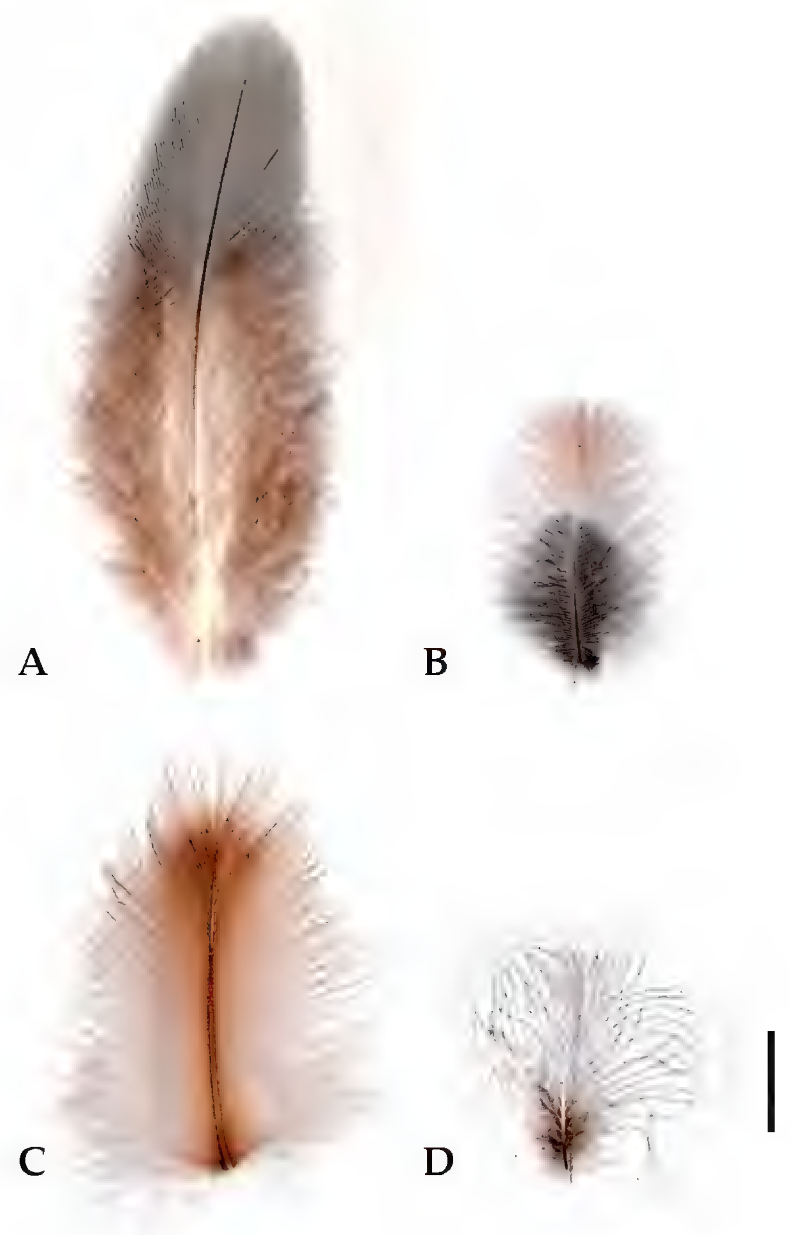

Fig. 4. Breast feathers in dorsal view. **A**. *C. palumbus*. **B**. *C. coccothraustes*. **C**. *P. carbo*. **D**. *T. ruficollis*. Scale bar = 1 cm.

plumulaceous part is present, too. *P. carbo* breast feathers show a continuous slender pennaceous vane with a broad outer rim. The feathers of *T. ruficollis* are very loose and show no connected vane.

The microstructure of the pennaceous region of the breast feathers of male sandgrouse (as well as in the few examined females) differs from that of other birds. The inner part of the vane is built by homogenous barbules which are intertwined by a twisted basis (Fig. 3G). The number of whorls differs by species and range in males on average from one (*S. tibetanus*), two (*P. quadricinctus*, *P. lichtensteinii*, *P. bicinctus*), three (*P. burchelli*, *P. exustus*, *P. guttularis*, *P. namaqua*) up to five (*P. orientalis*). The barbules are elongated (1mm in length), exhibit no barbicels and protrude from the ventral side of the feather vane (Fig. 3H) at an angle of 20°. In contrast, the outer rim consists of loose barb ends with elongated and completely straight barbules (Fig. 3I). The microstructure of the sandgrouse's back feathers exhibit barbules with and without barbicels which are interlocked (Fig. 3J) and resembles the normal structure of a pennaceous feather vane like breast feathers from *C. palumbus* or *C. coccothraustes*. *P. carbo* show a very fine-mesh inner vane of the same composition and a distinct outer rim with loose barbs and barbules. *T. ruficollis* exhibits uniform barbules without barbicels and a simple twisted basis which are not interlocked into each other. Feather microstructures of comparison species are shown in Fig. 5.

(c) Changes in feather configuration by wetting and structure of the barbules

The wetting changed the configuration of the morphology of the sandgrouse feathers in all species. The outer rim of the vane turned down to the ventral side of the feather (Fig. 6A) and formed a tube around the absorbed water. Only in *S. tibetanus* this mechanism was incomplete because of the broad and indistinct outer rim. The whorls at the basis of the barbules (Fig. 6B) unrolled by the contact with water (Fig. 6C) and changed the angle of the barbules to the feather vane on the ventral side from ca. 20° to ca. 90°. Both morphological changes from dry (Fig. 6D) to wet conditions (Fig. 6E) built a 3D-net of filamentous structures for storage of a large volume of water inside the feather structure. Both changes were completely reversible by drying. In *C. palumbus*, *C. coccothraustes* and *P. carbo* no morphological changes were observed in the feather structure by wetting. Barbules of *T. ruficollis* also unrolled their mono-twisted basis by contact with water but hardly changed their angle in relation to the feather vane.

The structure of the barbules (Fig. 6F) varied along their length. The medial and apical parts (Fig. 6G) showed a circular cross section with an outer layer and partly dark core coloration. The basal part of the barbules exhibited a crescent-shaped cross section (Fig. 6H) with an outer layer and two distinct inner layers with different structures. The keratin fibers of the layer of the concave side run in an angle of 90° to the fibers in the layer of the convex side. In SEM-pictures of freeze fractures from the basal part of barbules (Fig. 6I) an outer layer is not visible. The surface of the concave side of the basal part of the barbules has a fine dashed structure (Fig. 6I) in contrast to an amorphous shaped surface on that of the convex side (not shown).

Atomic force microscopic scans of cross sections from the basal part of the barbules (Fig. 6J) show two distinct layers, one at the convex side and another at the concave side. The two layers differ in their surface structure. In dry condition, the surface of both layers shows only minor differences in height of about 100nm (Fig. 6K–L). In wet condition the surface of the convex side raises up to ca. 500nm above the surface of the concave side (Fig. 6M–N).

(d) Wetting properties

The average material contact angle θ of breast feathers of *P. bicinctus* is 83.6° (n=13), of *P. carbo* 92.8° (n=14) and of untreated *C. coccothraustes* 96.5° (n=14). *C. coccothraustes* feathers which were dipped in acetone show a material contact angle of 94.5° (n=17) (Fig. 7A). Except for the hydrophilic sandgrouse feathers (θ = below

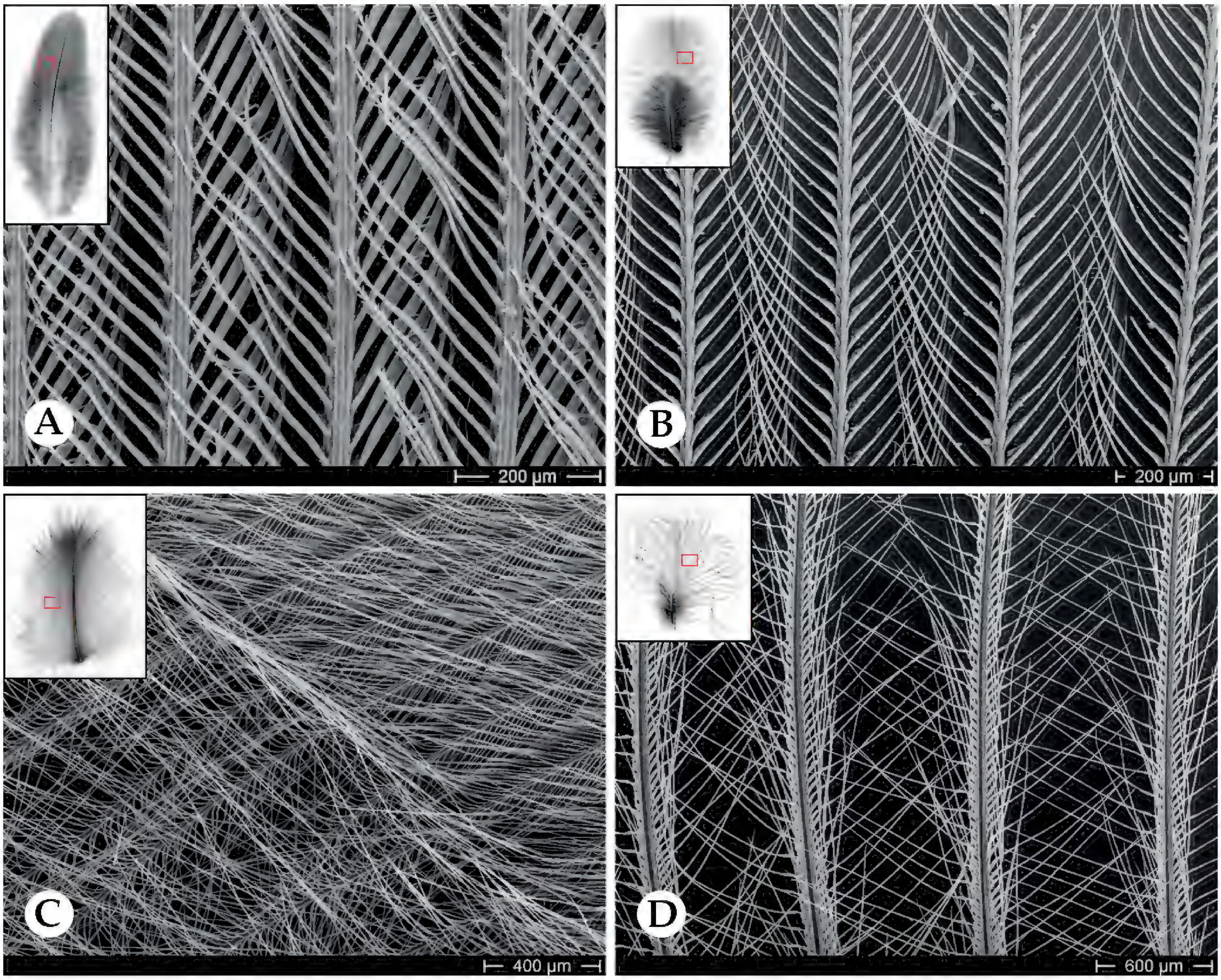

Fig. 5. Breast feather microstructure (barbs and barbules) in dorsal view. **A**. *C. palumbus*. **B**. *C. coccothraustes*. **C**. *P. carbo*. **D**. *T. ruficollis*.

90°), all material contact angles were hydrophobic (θ = over 90°). The contact angle of the sandgrouse differs significantly (two-tailed t-test, $p < 0.05$) from those of *P. carbo* and both *C. coccothraustes* samples.

Structural parameters and calculated (r+d)/r values of sandgrouse and non-sandgrouse species are listed in Table 1. The surface roughness r` of *P. bicinctus* breast feathers is 1.83 (706.650 µm^2 = real surface; 385.650 µm^2 = geometrical projected surface). Calculations based on the material contact angle θ and on the structural parameters resulted in the intrinsic contact angle θ* for all species (Table 2). Except for the hydrophilic sandgrouse feathers

Table 1. Structural parameters (n=15) of breast feather microstructure parameters according to Rijke (1970).

species	2r (in µm)	2d (in µm)	(r+d)/r	h
P. carbo (inner vane)	37.4	238.1	7.4	
P. carbo (outer rim)	33.1	352.3	11.7	
C. coccothraustes	24.9	257	11.3	
P. pyrrhula	21.4	240.8	12.2	
N. hollandicus	23.3	231.8	11	
A. apus	19.1	227.3	12.9	
P. bicinctus	17.1 (n=8)	240 (n=10)	15	107 µm (n=13)

©LIB

Table 2. Material θ and intrinsic contact angle θ* plus wetting properties of breast feathers according to calculations after Cassie & Baxter (1944) and Wenzel (1936).

species	material contact angle θ	intrinsic contact angle θ*	wetting properties
calculations according to Cassie & Baxter (1944)			
P. carbo (inner vane)	92.8°	151°	hydrophobic
P. carbo (outer rim)	92.8°	150.6°	hydrophobic
C. coccothraustes (natural)	96.5°	157.9°	hydrophobic
C. coccothraustes (aceton)	94.5°	157.3°	hydrophobic
calculations according to Wenzel (1936)			
P. bicinctus	83.6°	78.2°	hydrophilic

(θ* = below 90°), all intrinsic contact angles were hydrophobic (θ* = over 90°).

(e) Water absorption capacity

Sandgrouse feathers (*P. namaqua*, *P. bicinctus*) show their maximum water absorption capacity after 15 s. In contrast to the entire feathers, the water absorption of the *P. namaqua* feathers without an outer rim is reduced by about 30%. Feathers from non-sandgrouse species exhibit a low and linear increase of water intake (Fig. 7B).

(f) Numerical simulation

In the simulations, the falling water droplet decelerated differently depending on geometry (Fig. 7C–D). In the sandgrouse geometry, the droplet's fall ended after about 1.1 ms. The droplet then deformed, due to surface tension, into a spherical shape in an upward direction. The droplet in the varied geometry was falling for the full simulated time of 1.8ms. The water droplet in the sandgrouse geometry lost 0.2 mm in height until the sinking process was stopped.

DISCUSSION

It took a long time to clearly demonstrate water transport in sandgrouse for the first time and the underlying functional morphology also remained obscure for long. The latter could now be explained using new investigation methods, in particular the atomic force microscope. However, only different methodological approaches together will provide a complete picture of the water intake of sandgrouse.

Our results showed that besides the feather structure the **pterylography** of the breast and belly may also have an influence on the total water holding capacity. In contrast to closely related pigeons, sandgrouse showed a higher number of feathers within the breast and belly parts which overlapped more and orientated towards the featherless region in the middle of the abdominal side to form a maximum volume of feathers in this body region. Nitzsch (1840) investigated the pterylography of sandgrouses and pigeons but found no relevant differences except for the parallel form of the ventral feather tracts in sandgrouse which we also found.

Former investigations illustrated the **specialized feather structure** (Cade & MacLean 1967, Joubert & MacLean 1973) but did not mention the outer rim and its function in the feathers nor could they explain the movement of the barbules. In this work we were able to confirm that the outer rim plays an important role in the water holding capacity and that the movement of the microstructure is based on a hydroscopic motion due to a different swelling of two inner keratin layers. Joubert & MacLean (1973) also supposed that water enters the keratin structure and changes the structural formation, but they could not explain the biomechanical process. Our result is the first evidence of a directed hydroscopic motion for animals which is already well known for plants. In plants, the swelling and de-swelling of dead cells creates a repeatable movement that usually serves to spread spores, pollen or seeds. Two differently arranged cell layers of a tissue, each with a given direction of expansion (swelling anisotropy), cause a curvature or torsion of the overall structure. Interestingly, the thread-like partial fruits of the heron's bill (*Erodium* sp.) are very similar to the specialized barbules of sandgrouse in that they also have a basal spiralization, which unrolls completely when wetted (Sitte et al. 1998).

The material **contact angle** is normally measured by an optical goniometer (Barthlott & Neinhuis 1997) but this is only possible on plane surfaces (Marmur 2006). For measuring the material contact angle of feathers a tensiometer was used for the first time which is an established method in textile research (Hofmann 2002). By using this technique, we could confirm that sandgrouse exhibit hydrophilic feathers in contrast to other birds (including the cormorant). The feather structure indicates

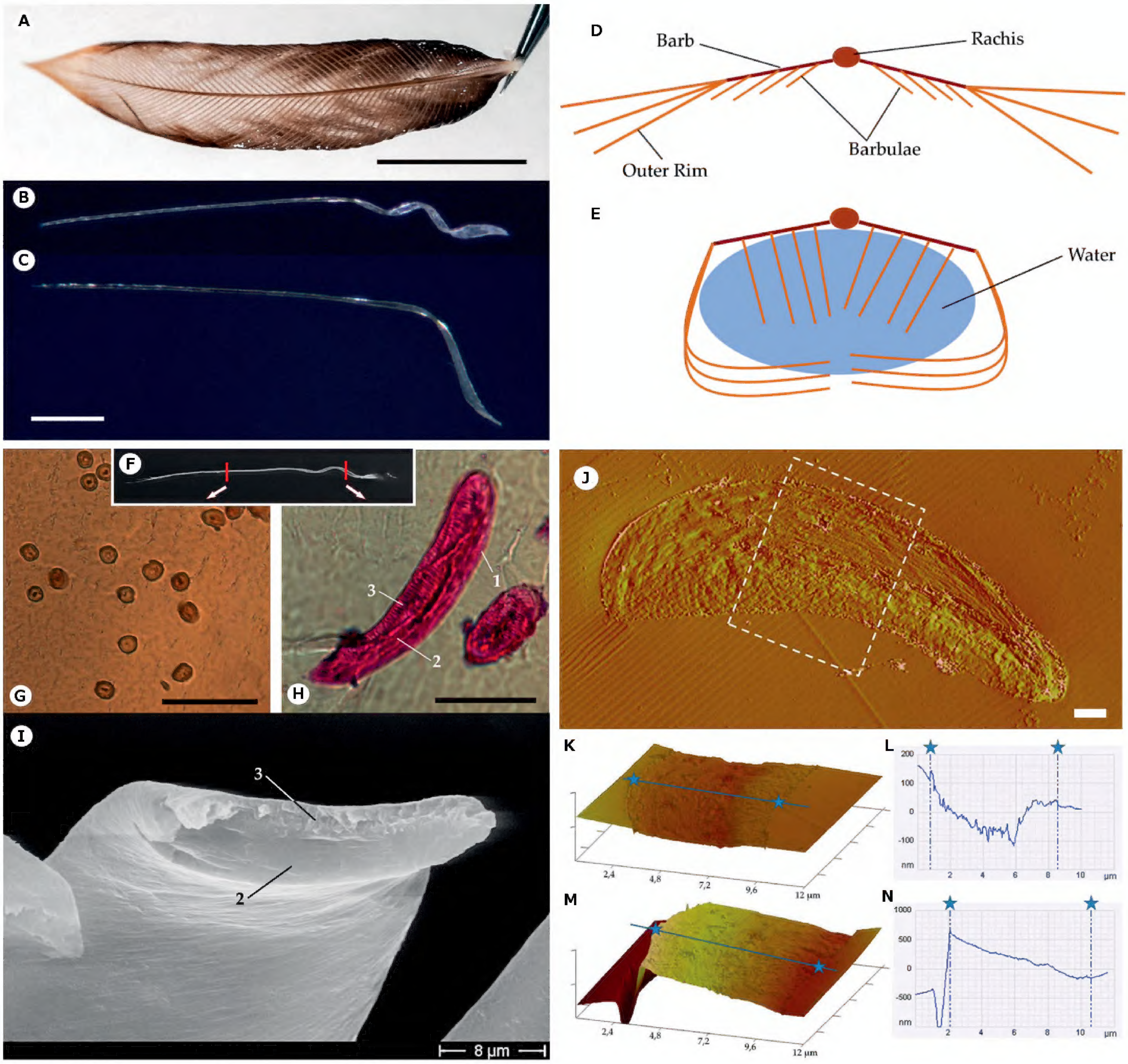

Fig. 6. A–E. Morphological changes in sandgrouse breast feathers. **A**. Outer rim of the vane turned down on the ventral side of the feather by wetting. **B**. Twisted basis of isolated barbule in dry conditions. **C**. Twisted basis of isolated barbule unrolled by contact with water. **D**. Idealized scheme of a feather in dry conditions. **E**. Idealized scheme of a feather in wet conditions. **F–I**. Internal composition of the barbules. **F**. Complete barbule with markings (red lines) of the cross section positions without scale. **G**. Light microscopic cross sections of the apical part of several barbules with distinct outer layers and partly dark core colorations (*P. namaqua*). **H**. Crescent-shaped cross section of the basal part of barbule with an outer layer (1) and two distinct inner layers (2 = concave side; 3 = convex side) with different fiber directions (*P. bicinctus*). **I**. SEM-picture of a freeze fracture of the basal part of the barbule without a visible outer layer and different surface structures of the breaking edges of the two inner layers. **J–N**. Atomic force microscope scans of the cross section of the basal part of a barbule (*P. namaqua*). **J**. Two-dimensional view on the surface structure in dry conditions with two distinct layers visible. White dashed square marks the area examined in K–N. **K**. Three-dimensional field of view of both layers when dry (three-dimensional view of the dashed field in J), with a corresponding height profile in L. **M**. Three-dimensional field of view of both layers when wet with a corresponding height profile in N. Line between the blue stars in K and M represents the respective path (through both layers) for the elevation profile in L and N. Scale bars: A = 0.5 cm; B–C = 200 µm; F–G = 50 µm; H = 20 50 µm; J = 2 µm.

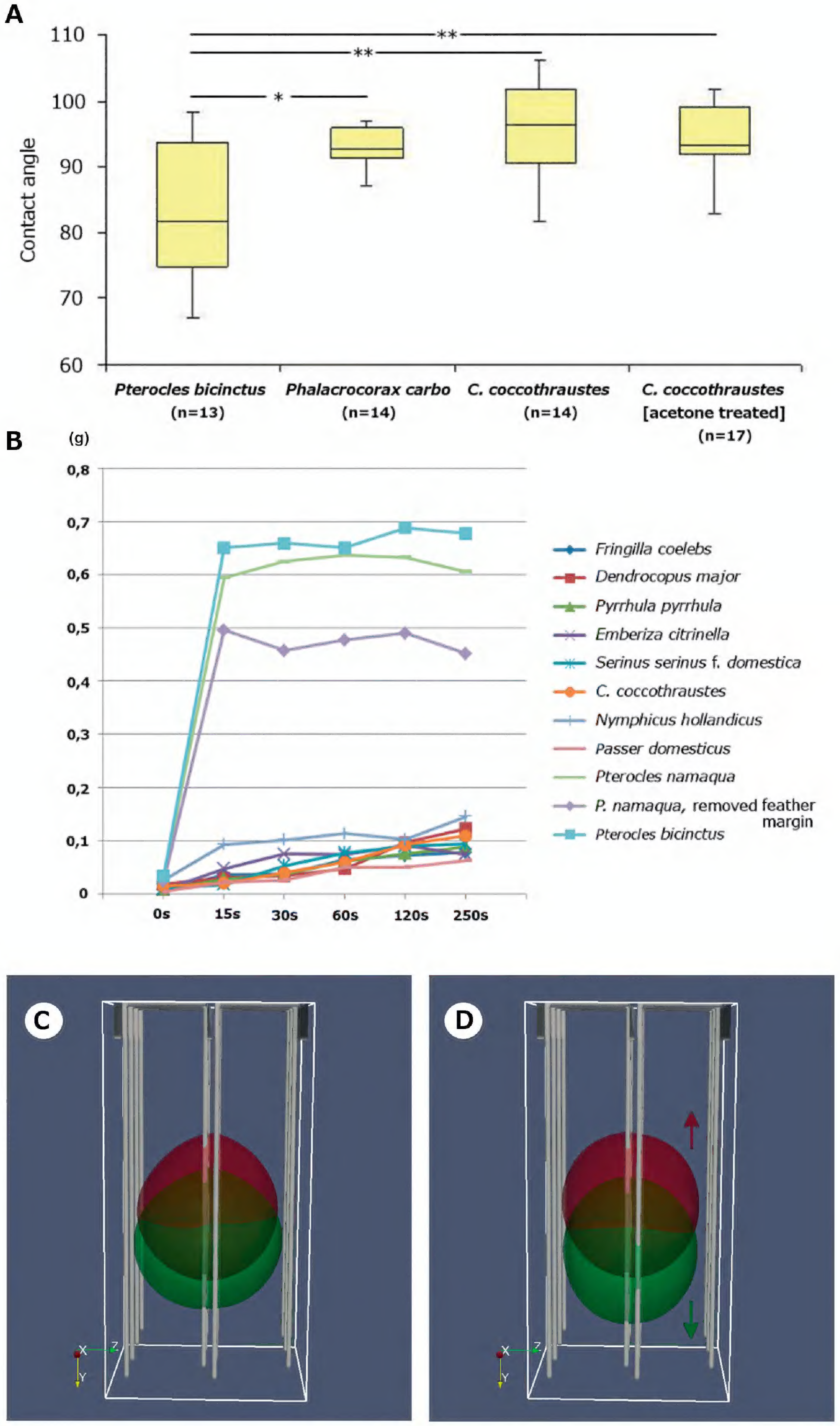

Fig. 7. A. Material contact angle of breast feathers from *P. bicinctus*, *P. carbo* and *C. coccothraustes* (natural condition and treated with acetone) measured by tensiometer. Two-tailed t-test * = $p < 0.05$, ** = $p < 0.01$. **B**. Water absorption capacity during the first 250 s of feathers from sandgrouse and non-sandgrouse species ($n=10$ per species). In contrast to the linear water absorption of the non-sandgrouse species over the whole time the sandgrouse show their maximum water uptake already after 15 s. Water absorption of sandgrouse feathers without the outer rim was reduced by about 30%. **C–D**. Overlapped droplet positions (red = sandgrouse-geometry, green=varied geometry) in lateral view of both numerical simulations at $t = 1.2$ ms (C) and $t = 1.8$ ms (D). Arrows in D indicate the direction of movement. While the droplet in the sandgrouse-geometry reached a steady state in the structure during the simulation time the droplet in the varied-geometry still fell downwards.

also a large (r+d)/r-value which suggests a poor water-repellent behavior, which is in contrast to non-sandgrouse species. The calculated intrinsic contact angles show so that the breast feathers of the sandgrouse differ from all others comparison species due to their hydrophilicity.

The sandgrouse feathers reached their maximum **water absorption** already within the first 15s and fluctuated afterwards. This contrasts with the much lower and linear increase of water uptake in the non-sandgrouse species which show no adaptations for water transport (feather structure and contact angle). In contrast to Thomas & Robin (1977), who did not have enough data to evaluate their hypothesis, we now demonstrate that the sandgrouse feathers show no evidence for a Michaelis-Menten saturation curve.

In the **numerical simulation** it could be shown that the microstructural parameters are optimized for water absorption. Already a minimal reduction of about 30% of the barbules in the digital geometry results in a strong reduction of the water retaining ability.

We could also show that in the evolution of sandgrouse the pterylography, the macro-, micro- and internal structures of the breast feathers as well as their wetting properties are highly optimized for the water transport which could be thought of as autapomorphy of the family that got subsequently lost in *S. tibetanus* because of its mountainous lifestyle. The evolution of this highly complex mechanism should be further investigated as it is a recent example of a substantial functional change of a complex structure.

Acknowledgements. We thank M. Griebel, H. Schmitz, T. Stegmaier, C. Kaya, A. Scherrieble, H. Roßmaier, L. Pastrik, M. Piefke, A. Hamm, I. Nüssle, R. van den Elzen, D. Stiels, J. Kasimir, K. Völker, M. Hendel, M. Lambertz, P. Comanns and C. Stommel. We would like to thank Dieter Wittmann for the idea for this work. The work was supported by grants from the German Federal Ministry of Education and Research (BMBF) to H.S. and from the German Research Foundation (DFG) to D.K.

REFERENCES

Amat JA, Masero JA (2007) The functions of belly-soaking in Kentish plovers *Charadrius alexandrinus*. Ibis 149: 91–97

Amat JA, Masero JA (2008) Belly-soaking: a behavioural solution to reduce excess body heat in the Kentish plover *Charadrius alexandrinus*. Journal of Ethology 27: 507–510

Begg GW, Maclean GL (1976) Belly-soaking in the White-crowned Plover. The Ostrich 47: 65

Cade TJ, MacLean GL (1967) Transport of water by adult sandgrouse to their young. The Condor 69: 323–343

Cassie ABD, Baxter S (1944) Wettability of porous surfaces. Transactions of the Faraday Society 40: 546–551

Croce R, Griebel M, Schweitzer MA (2010) Numerical simulation of bubble and droplet deformation by a level set approach with surface tension in three dimensions. International Journal for Numerical Methods in Fluids 62: 963–993

de Juana E (1997) Family Pteroclidiae (Sandgrouse). Pp 30–57 in: del Hoyo J Elliott A & Sargatal J (eds) Handbook of the Birds of the World, Vol. 4. Sandgrouse to Cuckoos. Lynx Edicions, Barcelona

Dove CJ (1997) Quantification of microscopic feather characters used in the identification of North American plovers. The Condor 99: 47–57

Grant GS (1981) Belly-soaking by Incubating Common, Sandwich, and Royal Terns. Journal of Field Ornithology 52: 244

Goutner V (1984) Belly-soaking in the Avocet. Ostrich 55: 167–168

Jackson JA, Schardien BJ (1981) Belly-soaking as a possible thermoregulatory mechanism in nesting Purple Martin. North American Bird Bander 6: 12–13

Joubert CSW, MacLean GL (1973) The structure of the water-holding feathers of the Namaqua Sandgrouse. Zoologica Africana 8: 141–152

Klocke D, Schmitz H (2012) Material properties of photomechanical infrared receptors in pyrophilous *Melanophila* beetles and *Aradus* bugs. Acta Biomaterialia 8: 3392–3399

Lloyd P, Durrans L, Gous R, Little RM, Crowe TM (2000) The diet and nutrition of the Namaqua sandgrouse, an arid-zone granivore. Journal of Arid Environments 44: 105–122

MacLean GL (1968) Field studies on the sandgrouse of the Kalahari desert. Living Bird 7: 209–235

MacLean GL (1983) Water Transport by Sandgrouse. BioScience 33: 365–369

MacLean GL (1975) Belly-soaking in the Charadriiformes. Journal of the Bombay Natural History Society 72: 74–82

Rijke AM (1970) Wettability and Phylogenetic Development of Feather Structure in Water Birds. The Journal of Experimental Biology 52: 469–479

Rijke AM (1972) The Water-Holding Mechanism of Sandgrouse Feathers. Journal of Experimental Biology 56: 195–200

Sangster G, Braun EL, Johansson US, Kimball RT, Mayr G, Suh A (2022) Phylogenetic definitions for 25 higher-level clade names of birds. Avian Research 13: 100027

Seymour RS, Ackerman RA (1980) Adaptations to Underground Nesting in Birds and Reptiles. American Zoologist 20: 437–447

Sick H (1937) Morphologisch-funktionelle Untersuchungen über die Feinstruktur der Vogelfeder. Journal für Ornithologie 85: 206–372

Sitte P, Ziegler H, Ehrendorfer F, Bresinsky A (1998). Strasburger. Lehrbuch der Botanik (34th ed.). Gustav Fischer Verlag, Stuttgart

Strong CM, Miyako S (2004) Black Skimmers Invade the Bay. Tideline 24: 1–3

Thomas DH, Robin AP (1977) Comparative studies of thermoregulatory and osmoregulatory behaviour and physiology of five species of sandgrouse (Aves: Pterocliidae) in Morocco. Journal of Zoology 183: 229–249

Wenzel RN (1936) Resistance of solid surfaces to wetting by water. Industrial and Engineering Chemistry 28: 988–994

BHL

Blank Page Digitally Inserted